University of Alberta

Seasonal and competitive factors controlling clonal regeneration of trembling aspen *(Populus tremuloides* Michx.*)*

by

Tara Lynn Mulak ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the

requirements for the degree of Master of Science

in

Forest Biology and Management

Department of Renewable Resources

Edmonton, Alberta

Spring 2006

Library and Archives Canada

Published Heritage Branch

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque et Archives Canada

Direction du Patrimoine de l'édition

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence
ISBN: 0-494-13855-6
Our file Notre référence
ISBN: 0-494-13855-6

NOTICE:
The author has granted a non-exclusive license allowing Library and Archives Canada to reproduce, publish, archive, preserve, conserve, communicate to the public by telecommunication or on the Internet, loan, distribute and sell theses worldwide, for commercial or non-commercial purposes, in microform, paper, electronic and/or any other formats.

The author retains copyright ownership and moral rights in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

AVIS:
L'auteur a accordé une licence non exclusive permettant à la Bibliothèque et Archives Canada de reproduire, publier, archiver, sauvegarder, conserver, transmettre au public par télécommunication ou par l'Internet, prêter, distribuer et vendre des thèses partout dans le monde, à des fins commerciales ou autres, sur support microforme, papier, électronique et/ou autres formats.

L'auteur conserve la propriété du droit d'auteur et des droits moraux qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

In compliance with the Canadian Privacy Act some supporting forms may have been removed from this thesis.

While these forms may be included in the document page count, their removal does not represent any loss of content from the thesis.

Conformément à la loi canadienne sur la protection de la vie privée, quelques formulaires secondaires ont été enlevés de cette thèse.

Bien que ces formulaires aient inclus dans la pagination, il n'y aura aucun contenu manquant.

Canada

In loving memory of my Dad and for my Mom, Marshall and Janet Mulak

Abstract

A field study and two greenhouse studies examined root suckering of aspen (*Populus tremuloides* Michx.). A field study examined the impact of residual trees (0, 500 or 1,500 sph) and season of cutting (bud set, dormant, bud flush) on re-suckering of ten-year-old aspen stands. Suckering decreased with increasing residual density, while there was little impact of season of cutting on suckering. The first greenhouse study tested the effects of *C. canadensis* and *C. cornuta* litter on root suckering. Litter had little effect on suckering; however, *C. canadensis* litter delayed sucker emergence. The second greenhouse study examined whether aspen suckering is influenced by the direct competition of *C. canadensis*, and secondly, if additional nutrients can negate some of the competitive effects. *Calamagrostis canadensis* sod did not impact the initiation of suckers, but resulted in decreased numbers of suckers emerging after 30 days. The addition of nutrients was not beneficial to suckering.

Acknowledgements

I would like to give my sincerest thanks to my supervisors Dr. Victor Lieffers and Dr. Simon Landhäusser for their support and guidance throughout the course of my degree. Thank you for all your knowledge and encouragement and always having time to answer my many questions. You made my time at the University of Alberta that much more rewarding.

My thanks to everyone in the Silviculture Lab. Erin Fraser, Heather Fish and Lee Martens, you are much more than just colleagues. If not for you I don't think I would have grown as much as I have and things would not have been anywhere near as interesting. And thank you Pak Chow for all your help and support. I would also like to thank all the summer students who were involved with my studies, especially Erin Smith; there was never a dull moment.

I would also like to thank all the other people who helped me during the course of my degree: Roger Butson and Dave Fox of Alberta Pacific Forest Industries Inc. and Carl Alexandruk, formerly of Daishowa-Marubeni International Ltd., for helping me located my field sites, the brushing crews from Sundance Reforestation Ltd. and Clayborne Contracting who cut all my trees and Bruce Alexander from the Agriculture Forestry greenhouse at the University of Alberta for giving me so much of his time and help.

Thank you to my family and friends. Thank you Mom, for your never ending support and encouragement though all my years of school. For my Dad, who put nature in my heart, I miss you dearly. My sister Tory, I've learned to expect the unexpected, thank you for all you help and support. Lannie, you were there through it all. You made me believe in myself because you never stopped believing in me. Thank you. In loving memory of my grandparents, if not for them none of this would have been possible. Thank you to grandma, you taught me to be strong willed and to always stand up for myself. Finally, thank you to all my friends who always supported me while I was in 'Tree Land'. I love you all.

Financial support for my studies was generously provided by Ainsworth Lumber Inc., Alberta Pacific Forest Industries Inc., Alberta Plywood Ltd. (West Fraser Mills), Daishowa-Marubeni International Ltd., Louisiana Pacific Corp., Millar Western Industries Ltd., Weyerhaeuser Canada Ltd. and was matched by Natural Sciences and Engineering Research Council of Canada (NSERC).

TABLE OF CONTENTS

CHAPTER I: General Introduction 1
Trembling Aspen Regeneration 1
Residual Density and Time of Thinning 1
Litter and Competition 3
Trembling Aspen Management 5
References 8

CHAPTER II: Aspen regeneration in relation to residual density and season of cut 12
Introduction 12
Methods and Materials 14
Pre-treatment Measurements 15
Post treatment measurements 16
Root Carbohydrates 16
Experimental design and statistical analysis 17
Results 18
Residual aspen density treatment 18
Time of thinning 19
Root Carbohydrates 19
Effect of residual density on root carbohydrate reserves 19
Sugar 19
Starch 20
Total non-structural carbohydrates (TNC) 20
Effect of time of thinning on root carbohydrate reserves 21
Sugar 21
Starch 21
Total non-structural carbohydrates (TNC) 21
Shrubs 22
Discussion 22
Residual aspen density treatment 22

Time of thinning 24
Shrubs 25
References 32

CHAPTER III: Effects of *Calamagrostis canadensis* and *Corylus cornuta* on Trembling Aspen (*Populus tremuloids* Michx) suckering 35
Introduction 35
Methods and Materials 37
Litter Experiment 38
Competition Experiment 39
Statistical Analysis 41
Results 41
Litter Experiment 41
Competition Experiment 42
Discussion 43
Conclusion 45
References 54

CHAPTER IV: Research Summary, Implications and Future Research 58
Residual Density and Time of Thinning 58
Litter and Competition 60
Management Implication 62
Future Research 63
References 65

APPENDIX A. Means of aspen response variables. 67
Table A1: Density of total amount of regeneration and clusters with separated into stump sprouts and suckers for each treatment (n=27). Treatment means with the same letter in columns and within treatments are not significantly different. 68
Table A2: Densities of stump sprouts, suckers and total regenerating stems (stump sprouts and suckers) in relation to time of thinning and number of residual stems retained (n=9) 68

Table A3: Total leaf area and height of regeneration including standard errors for each combination of time of thinning and density of residual stems (n=9). 68

APPENDIX B. Means of response variables for shrubs and grass. 69

Table B1: Densities of re-sprouting after the first growing season after treatment for alder (n=3), hazel (n=3) and willow (n=10). Grass (*Calamagrostis canadensis*) percentage cover was also estimated (n=10). (± standard errors). 70

Table B2: Heights of re-sprouting alder (n=3), hazel (n=3) and willow (n=10) and estimated % grass (*Calamagrostis canadensis*) cover including standard errors. (± standard errors). 70

Table B3: Pre- and post treatment average % grass (*Calamagrostis canadensis*) cover (n=10) in relation to time of thinning aspen and season of cut. (± standard errors). 70

LIST OF TABLES

Table 2.1. Stem density of shrubs, pre-thinning (Pre-) and post thinning (Post) of the aspen overstory, after the first growing season, in relation to density of residual aspen trees and season of thinning; alder (n=9), hazel(n=9) and willow (n=30) and percent grass cover (*Calamagrostis canadensis*) (n=30). Treatment means with the same letter in columns and within the residual density and time of thinning treatments are not significantly different..... 26

Table 2.2. Height of shrubs after the first growing seasoning after thinning; alder (n=9), hazel (n=9) and willow (n=30) and percent grass (*Calamagrostis canadensis*) cover (n=30). Treatment means with the same letter in columns and within the residual density and time of thinning treatments are not significantly different..... 27

LIST OF FIGURES

Figure 2.1: Effects of residual density of aspen on aspen regeneration one year after thinning A. Density of regeneration as the proportion of stump sprouts and suckers presented as the total number of stems and total number of clusters. Different letters over the bar indicate significant differences in the sum of stump sprout and sucker densities determined for the total number of stems and clusters. Total stem and cluster density were analyzed separately (n=27); B. Height of regenerating stems (summing suckers and stump sprouts) (n=27); and C. Leaf area index of regenerating stems (summing stump sprouts and suckers) (n=27). Means with the same letter are not significantly different..... 28

Figure 2.2: Effects of time of thinning on aspen regeneration one year after thinning A. Density of regeneration as the proportion of stump sprouts and suckers presented as the total number of stems and total number of clusters. Different letters over the bar indicated significant differences in the sum of stump sprout and sucker densities determined for the total number of stems and clusters. Total stem and cluster density were analyzed sparately (n=27); B. Height of regenerating stems (summing suckers and stump sprouts) (n=27); and C. Leaf area index of regenerating stems (summing stump sprouts and suckers) (n=27). 29

Figure 2.3: Effects of residual density treatment on carbohydrate concentrations IN roots associated with residual trees (-r) and from roots associated with regenerating sprouts (-s) after regeneration started in July. A. sugars, B. starch and C. total nonstructural carbohydrates. Collections from roots emanating from residual trees or near regenerating sprouts started in September 2003. Collections from roots associated with sprouts were collected in July and September 2004 in the first year after thinning. For September 2003 and April 2004 n=5, for May 2004 n=10, for July and September 2004 n=15. 30

Figure 2.4: Effects of time of thinning on carbohydrate concentrations IN roots associated with residual trees (-r) and from roots associated with regenerating sprouts (-s) after regeneration started in July. A. sugars, B. starch and C. total nonstructural carbohydrates. Collections from roots emanating from residual trees or near regenerating sprouts started in September 2003. Collections from roots associated with sprouts were collected in July and September 2004 in the first year after thinning. For each collection time n=15. 31

Figure 3.1: Total number of emerged aspen suckers found above and below the *C. canadensis* or *C. cornuta* litter layers or in the controls after 30 and 56 days of growth (n=11). The number of suckers found above and below the litter were analyzed separately. Treatment means with the same letter are not significantly different 46

Figure 3.2: Average height of aspen suckers that had emerged above the litter layer of *C. canadensis* or *C. cornuta* or above the soil of the control after 30 and 56 days of growth (n=11). Means with the same letter are not significantly different. 47

Figure 3.3: Average root collar diameter of aspen suckers that had emerged above the *C. canadensis* or *C. cornuta* litter or above the soil for the control, after 30 or 56 days of growth (n=11). Means with the same letter are not significantly different. 48

Figure 3.4: Total leaf area of aspen suckers that had emerged above the *C. canadensis* or *C. cornuta* litter or above the soil for the control, after 30 or 56 days of growth (n=11). Means with the same letter are not significantly different..... 49

Figure 3.5: Total weight of aspen suckers that had emerged above the *C. canadensis* or *C. cornuta* litter or above the soil for the control, after 30 or 56 days of growth (n=11). Means with the same letter are not significantly different..... 50

Figure 3.6: The average number of aspen suckers that emerged above the soil and suckers still below the soil (non-emerged, elongated root buds) from root systems

with or without *C. canadensis* sods (n=16). The number of emerged and non-emerged suckers were analyzed separately. Treatment means with the same letter are not significantly different 51

Figure 3.7: Average weight of aspen suckers emerged above the soil, from root systems with or without *C. canadensis* sods (n=16). Means with the same letter are not significantly different 52

Figure 3.8: Total leaf area of aspen suckers per planter box emerged above the soil, from root systems with or without *C. canadensis* sods (n=16). Means with the same letter are not significantly different 53

CHAPTER I

General Introduction

Trembling Aspen Regeneration

Trembling aspen (*Populus tremuloides* Michx.), is widely distributed throughout North America and can exist as pure stands, or in mixtures with other tree species such as white spruce (*Picea glauca* Moench Voss) (Baker 1918, Day 1944, Crouch 1981, Bates et al. 1989, Doucet 1989). Aspen is an early successional, fast growing, shade intolerant clonal tree species with an extensive lateral root system that is concentrated in the upper 30 cm of the soil profile (Day 1944, Tew 1970). Root systems vary in size and can cover several hectares and a single root system can support anywhere from a single tree to thousands of trees per hectare (Kemperman and Barnes 1976, Steneker 1976). Aspen regenerates primarily by vegetative propagation through root suckers. Sprouts emanating from stumps and root collars (only in juvenile trees) and seedling establishment is less common (Baker 1918, Day 1944, Kemperman 1978, Schier et al. 1985, Mowrer 1988, Doucet 1989, Bates et al. 1993). Root suckers arise from lateral roots 0.04 – 9.00 cm in diameter found within 15 cm of the soil surface (Baker 1918, Day 1944, Kemperman 1978, Schier et al. 1985, Shepperd 1993). The shallow root system regenerates aggressively after a disturbance, such as fire or clearcutting, removes the above ground portion of the stand, producing anywhere from 4,000 to well over 100,000 stems per hectare (sph) (Zehngraff 1949, Stoeckeler and Macon 1956, Farmer 1962, Jones and Trujillo 1975, Steneker 1976, Crouch 1981, Schier et al. 1985, Crouch 1986, Bates et al. 1993, DesRochers and Lieffers 2001, Frey et al. 2003).

Residual Density and Time of Thinning

Aspen sucker regeneration is closely related to apical dominance. When apical dominance is maintained sucker initiation is inhibited (Farmer 1962, Frey et al. 2003).

This inhibition is mediated by the activity of two important groups of hormones, auxins and cytokinins (Farmer 1962, Lavertu et al. 1994, Frey et al. 2003). Auxins are produced in the above ground tissues (swelling buds, growing shoots and leaves) and are translocated to the roots where they are known to inhibit root sucker formation (Farmer 1962, Eliasson 1971, Schier and Zasada 1973, Schier et al. 1985, Frey et al. 2003). Cytokinins counteract auxin activity (Frey et al. 2003). Cytokinins are produced in the actively growing root tips and exhibit polar movement towards the stem where they play a role in shoot elongation and growth (Farmer 1962, Eliasson 1971, Fitzgerald 1983, Frey et al. 2003). A disturbance that removes or kills the above ground portions of a clone thereby removes apical dominance and skews the auxin:cytokinin ratio in favor of cytokinins. The disruption of the flow of auxin to the roots and the increase in the proportion of cytokinins in the root tissue is thought to promote shoot development on the roots (Farmer 1962, Eliasson 1971, Fitzgerald and Hoddinott 1983, Schier et al. 1985, Frey et al. 2003). The amount of aspen suckering is therefore linked to the degree of stand or clone disturbance (Steneker 1976, Schier and Smith 1979, Lavertu et al. 1994). The greater the above ground portion of a clone that is removed or killed by a disturbance the greater the amount of regeneration by suckering (Stoeckeler and Macon 1956, Steneker 1976, Huffman et al. 1999). Complete removal of the canopy (clearcutting) is recognized as the preferred silvicultural treatment for regenerating aspen stands (Zehngraff 1949, Farmer 1962, Schier and Smith 1979, Doucet 1989, Bates et al. 1993, Frey et al 2003). Complete removal is thought to stimulate the greatest number of suckers (Zehngraff 1949, Farmer 1962, Schier and Smith 1979, Doucet 1989, Bates et al. 1993, Frey et al 2003).

Root carbohydrate reserves also play a role in aspen regeneration in relation to the season in which the aspen are cut. It is accepted that apical dominance not carbohydrate reserves plays the dominant role in sucker initiation (Farmer 1962, Schier and Zasada 1973, Schier et al. 1985, Bell et al. 1999, Frey et al. 2003). However, the total nonstructural carbohydrate (TNC) reserves in the roots of the aspen at time of cutting are thought to play an important role in the growth and vigor of the suckers. Once suckers are initiated they are sustained by the carbohydrate reserves in the parent root systems

until they emerge from the soil. After emergence, suckers need to produce leaf area and begin to photosynthesize (Schier and Zasada 1973, Schier et al. 1985, Bates et al. 1989, DesRochers and Lieffers 2001, Landhäusser and Lieffers 2002). There is a general pattern of root carbohydrate concentration changes throughout the growing season. Typically, root carbohydrates are found to be low in the spring and early summer at the time of leaf flush, build throughout the growing season and reach the highest levels in late summer and early fall (Farmer 1962, Tew 1970, Schier and Zasada 1973, Bates et al. 1989, Bell et al. 1999, Landhäusser and Lieffers 2002). By late fall and winter, however, the carbohydrate reserves in aspen roots are greatly depleted (Landhäusser and Lieffers 2002). For mature aspen stands there are mixed results regarding which season of harvest produces the highest or lowest density of regenerating stems. Several studies have found higher sucker numbers and greater vigor resulting from winter harvest (Zasada 1946, Zehngraff 1949, Bates et al. 1993, Bell et al. 1999) while other studies found greater sucker densities resulting from summer harvests when compared to winter harvest (Bella 1986). These varying responses have been associated with high root carbohydrate reserves during the winter months or were thought to be the result of confounding effects of traffic impact on the root system during the summer compared to winter when soils are frozen.

Litter and Competition

Aspen is known to regenerate aggressively after a disturbance, however simply cutting aspen stands at any time of year or stand condition does not always result in a fully stocked regenerating stand (Frey et al. 2003). A thick organic litter (LFH) layer can be detrimental to aspen suckering. It has been well documented that a thick LFH layer can insulate soils, thereby producing colder soil conditions in northern climates (Hogg and Lieffers 1991, Landhäusser and Lieffers, 1998). *Calamagrostis canadensis* (Michx.) Beauv is known to negatively impact aspen regeneration (Lieffers et al. 1993, Landhäusser and Lieffers 1998, Powell and Bork 2004) and high densities of *Corylus Cornuta* Marsh (beaked hazelnut) can inhibit tree reproduction (Tappeiner and Alm 1972, Best et al. 2003). Dense beds of *C. canadensis* can produce thick sods and dense layers

of insulating litter after several years of growth (Lieffers et al. 1993) and *C. cornuta* which is a medium sized shrub can produce dense stands with significant leaf cover and annual litter deposits. *Calamagrostis canadensis* litter has been shown to have negative effects on aspen seedling growth (Landhäusser and Lieffers 1998). The accumulation of litter might also result in a physical barrier to emerging suckers. The removal of the LFH layer has been shown to improve aspen suckering (Alban et al. 1994, Lavertu et al. 1994, Stone and Elioff 1998).

Although aspen regeneration can be prolific, competing vegetation can interfere with establishment and growth of suckers. *Calamagrostis canadensis* is a fierce competitor in the juvenile stages of many boreal forest tree species. *Calamagrostis canadensis* is quick to colonize disturbed areas through rhizome spread and seeds, and can dominate 3 years after disturbance (Lieffers et al. 1993). If sods of the grass are already well developed at time of disturbance, the grass will dominate in only one year. Rhizome growth and sod formation is typically within 4-5 cm of the soil surface, but in northern Alberta cutovers it was observed to depth of 15 cm (Lieffers et al. 1993). Aspen roots where sucker buds are formed are located at the same rooting depth (Baker 1918, Day 1944, Kemperman 1978, Schier et al. 1985, Shepperd 1993), thus this grass is in direct competition for space and nutrient resources. Many studies have demonstrated reduced growth of aspen seedlings when associated with *C. canadensis* (Lieffers et al. 1993, Landhäusser and Lieffers 1998, Powell and Bork 2004). It is unclear if nutrient resources such as nitrogen are in short supply because of the presence of the nutrient demanding *C. canadensis* (Landhäusser and Lieffers 1998). Studies have shown improved aspen growth with fertilization (King et al. 1999, Fraser et al. 2002) however, reliance of aspen suckers on the nutrient reserves stored in the parent roots system may provide another avenue for suckers to receive nutrients.

Inhibitory allelopathic effects have been linked to both residual litters and live vegetation. Researchers have speculated that *C. canadensis* has allelopathic effects towards aspen sucker and seedling growth (Landhäusser and Lieffers 1998, Frey et al. 2003). Allelopathy has been observed from agricultural grass species following crop rotation (Rice 1984, Oueslati 2003), and Winder and Macey (2001) demonstrated

autotoxicity of *C. canadensis*. In aspen stands with a dense understory of *C. cornuta*, there can be a significant layer of litter from this shrub. This litter may also have allelopathic effects towards aspen, similar to the allelopathic effects of various shrub and broadleaf species noted by Rice (1984).

Trembling Aspen Management

Aspen is a highly competitive species. If it establishes at high densities, it is difficult to convert these stands to conifer plantations (Day 1944). In mixedwood stands of aspen and white spruce, managers try to control the density of regenerating aspen in an attempt to establish white spruce. Aspen is usually manually removed or chemically treated with herbicides. Manual cutting of the juvenile stems generally results in re-sprouting (mostly of stump sprouts) and managers might have to return to the site for re-treatment (Bell et al. 1999).

Maintaining a residual aspen canopy could control the amount of resulting aspen regeneration. In mature aspens stands there is a strong relationship between the number of residual stems and the density of regenerating aspen. Many studies have shown reduced regeneration when a portion of the stand remains uncut. The greater the density of residual stems the fewer the regenerating stems (Stoeckeler and Macon, 1956, Steneker 1976, Huffman et al. 1999). Huffman et al. (1999) found that in 7- and 8-year-old regenerating stands, as residual aspen cover increased, the number of regenerating stems significantly decreased. Schier and Smith (1979) found that partial cutting (67% of original basal area removed) in a 55-year-old stand resulted in a 53% decrease in regenerating stems compared to a clearcut and Stoeckeler and Macon (1956) found that regenerating stands that had 20% and 40% of the original basal area retained after harvest, had on average 4,250 and 5,288 fewer suckers per ha than stands that had been clearcut.

The season or phenological stage when aspen is manually removed could also play a role in the density of aspen regeneration. Many studies have shown variation in the number and vigor of suckers emerging after mature aspen stands were harvested at different times of the year. Following summer harvest, Zengraff (1946) found there was

on average 30,765 fewer stems per hectare than the regeneration following winter cuts. Bell et al. (1999) found that regeneration density and height growth from summer cuts was lower compared to winter and spring cuts and Bates et al. (1993) found height growth to be reduced by 30 cm in summer cuts compared to winter cuts. Landhäusser and Lieffers (2002) found that saplings cut in spring had lower height growth and leaf area development than those cut in fall. Conversely, Bella (1986) found that the density in the first year following summer harvest was nearly double that of winter harvest. These results have been linked to the seasonal changes in hormone concentrations and root carbohydrate reserves.

Removal of the accumulated litters of *C. canadensis* and *C. cornuta* could be advantageous to aspen regeneration. Aspen seedlings grown without the presence of *C. canadensis* litter had improved root caliper growth and stem and leaf weight over aspen seedlings grown in association with *C. canadensis* litter (Landhäusser and Lieffers 1998). After clearcutting, Stone and Elioff (1998) found that in plots where the forest floor was removed sucker density was three times that of plots with the forest floor remaining. Alban et al. (1994) observed an average of 16.7 more suckers/m^2 (167,000/ha) on plots where the forest floor had been removed. In 4 m^2 plots, scarification resulted in an average of 48.7 more suckers per plot (121,750/ha) than plots without scarification (Lavertu et al. 1994). Removal of litter results in greater heat transfer into the soil in spring and early summer resulting in higher soil temperatures during the growing season (Hogg and Lieffers 1990). The removal of litter would also remove any potential allelopathic effects that the *C. canadensis* and *C. cornuta* litters may produce. It is not clear however, if *C. canadensis* and *C. cornuta* litter exhibits allelopathic effects on aspen regeneration over other more documented effects of litter such as acting as a thermal insulator. Extracts from *C. canadensis* straw have been shown to reduce its own growth and could have detrimental effects on aspen suckering and sucker growth (Winder and Macey 2001). *Corylus cornuta* litter could possible produce similar negative effects towards aspen establishment and growth as that of *Rubus idaeus* var. *strigosus* (raspberry) and *Prunus serotina* (black cherry) or the dripline under the canopy of *Juglans nigra* (black walnut) (Rice 1984).

Control of *C. canadensis* competition could have beneficial effects on aspen regeneration. Aspen seedlings grown without *C. canadensis* grew much better than seedlings grown together with *C. canadensis* (Landhäusser and Lieffers 1998, Powell and Bork 2004). Mortality of aspen was less and height growth greater when aspen were grown in the presence of shrubs and other trees, than when it was grown in association with *C. canadensis* (Lieffers et al. 1993). It remains unclear if *C. canadensis* plants exhibit allelopathic effects on aspen regeneration in addition to the direct competition for water, light, nutrients and growing space. However, allelopathy of wild oat grass (*Danthonos compressa* Aust.) in association with other species was suspected to contribute to poor vigor of aspen seedlings (Horesely 1976).

The overall objective of this thesis research was to investigate factors which influence sucker regeneration of aspen. The specific objectives were: (1) to examine the influence of clone phenology and residual stem density on rates of re-suckering and re-sprouting after thinning of juvenile aspen stands; (2) to assess the effects of *C. canadensis* and *C. cornuta* litter on suckering of aspen; and (3) to observe the direct effects of competition from *C. canadensis* and fertilization on aspen root suckering and growth.

References

Alban, D.H., Host, G.E., Elioff, J.D., and Shadis, D. 1994. Soil and vegetation resonse to soil compaction and forest floor removal after aspen harvesting. USDA For. Serv. Res. Pap. NC-315.

Baker, F.S. 1918. Aspen reproduction in relation to management. J. For. 16: 389-398.

Bates, P.C., Blinn, C.R., and Alm, A.A. 1993. Harvesting impacts on quaking aspen regeneration in northern Minnesota. Can. J. For. Res. 23: 2403-2412.

Bates, P.C., Blinn, C.R., Alm, A.A., and Perala, D.A. 1989. Aspen stand development following harvest in the Lake States Region. North. J. Appl. For. 6: 178-183.

Bell, F.W., Pitt, D.G., Morneault, A.E., and Pickering, S.M. 1999. Response of immature trembling aspen to season and height of cut. North. J. Appl. For. 16(2): 108-114.

Bella, I.E. 1986. Logging practices and subsequent development of aspen stands in east-central Saskatchewan. For. Chron. 62: 81-83.

Best, J.N., Bork, E.W., and Cool, N.L. 2003. Initial beaked hazel growth responses following protection from ungulate browsing. J. Range. Manage. 56: 455-460.

Crouch, G.L. 1981. Regeneration on aspen clearcuts in northwestern Colorado. USDA For. Serv. Res. Note RM-407.

Crouch, G.L. 1986. Aspen regeneration in 6- to 10-year-old clearcuts in southwestern Colorado. USDA For. Serv. Res. Note RM-467.

Day, M.W. 1944. The root system of aspen. Am. Midl. Nat. 32:502-509.

DesRochers, A., and Lieffers, V.J. 2001. Root biomass of regenerating aspen (*Populus tremuloides*) stands of different densities in Alberta. Can. J. For. Res. 31: 1012-1018.

Doucet, R.1989. Regeneration silviculture of aspen. For. Chron. 65: 23-27.

Eliasson, L. 1971. Growth regulators in *Populus tremula* III. Variation of auxin and inhibitor level in roots in relation to root sucker formation. Physiol. Plant. 25: 118-121.

Farmer, R.E. 1962. Aspen root sucker formation and apical dominance. For. Sci. 8: 403-410.

Fitzgerald, R.D., and Hoddinott, J. 1983. The utilization of carbohydrates in aspen roots following partial or complete top removal. Can. J. For. Res. 13: 685-689.

Fraser, E.C., Lieffers, V.J., Landhäusser, S.M., and Frey, B.R. 2002. Soil nutrition and temperature as drivers of root suckering in trembling aspen. Can. J. For. Res. 32: 1685-1691.

Frey, B.R., Lieffers, V.J., Landhäusser, S.M., Comeau, P.G., and Greenway, K.J. 2003. An analysis of sucker regeneration of trembling aspen. Can. J. For. Res. 33: 1169-1179.

Hogg, E.H., and Lieffers, V.J. 1991. The impact of *Calamagrostis canadensis* on soil thermal regimes after logging in northern Alberta. Can. J. For. Res. 21: 387-394.

Horsely, S.B. 1976. Allelopathic inhibition of black cherry by fern, grass goldenrod, and aster. Can. J. For. Res. 7: 205-216.

Huffman, R.D., Fajvan. M.A., and Wood, P.B. 1999. Effects of residual overstory on aspen development in Minnesota. Can. J. For. Res. 29: 284-289.

Jones, J.R., and Trujillo, D.P. 1975. Development of some young aspen stands in Arizona. USDA For. Serv. Res. Pap. RM-151.

Kemperman, J.A. 1978. Sucker-root relationships in aspen. Ontario MNR. For. Res. Note 12.

Kemperman, J.A., and Barnes, B.V. 1976. Clone size in American aspens. Can. J. Bot. 54: 2603-2607.

King, J.S., Pregitzer, K.S., and Zak, D.R. 1999. Clonal variation in above- and below-ground growth responses of *Populus tremuloides* Michaux: Influence of soil warming and nutrient availability. Plant Soil 217: 119-130.

Landhäusser, S.M., and Lieffers, V.J. 1998. Growth of *Populus tremuloides* in association with *Calamagrostis candensis*. Can. J. For. Res. 28: 396-401.

Landhäusser, S.M., and Lieffers, V.J. 2002. Leaf area renewal, root retention and carbohydrate reserves in clonal tree species following above-ground disturbance. J. Ecol. 90: 658-665.

Lavertu, D., Mauffette, Y., and Bergeron, Y. 1994. Effects of stand age and litter removal on the regeneration of *Populus tremuloides*. J. Veg. Sci. 5: 561-568.

Lieffers, V.J., Macdonald, S.E., and Hogg, E.H. 1993. Ecology of and control strategies for *Calamagrostis canadensis* in boreal forest sites. Can. J. For. Res. 23: 2070-2077.

Oueslati, O. 2003. Allelopathy in two durum wheat (*Triticum durum* L.) varities. Agric. Ecosystems and Environ. 96: 161-163.

Mowrer, H.T. 1988. Is managing aspen density worthwhile? In: Proceedings – Future Forests of the Mountain West: A stand culture symposium. W.C. Schmidt (compiler). USDA For. Serv. Gen. Tech. Rep. INT-243. pp. 201-209.

Powell, G.W., and Bork, E.W. 2004. Competition and facilitation in mixtures of aspen seedlings, alfalfa, and marsh reedgrass. Can. J. For. Res. 34: 1858-1869.

Rice, E.L. 1984. Allelopathy 2nd ed. Academic Press, Inc., Orlando, Fla.

Schier, G.A., and Zasada, J.C. 1973. Role of carbohydrate reserves in the development of root suckers in *Populus tremuloides*. Can. J. For.Res. 3: 243-250.

Schier, G.A., and Smith, A.D. 1979. Sucker regeneration in Utah aspen clone after clearcutting, partial cutting, scarification, and girdling. USDA For. Serv. Res. Note INT-253.

Schier, G.A., Jones, J.R., and Winokur, R.P. 1985. Vegetative regeneration. *In* Aspen: ecology and management in the western United States. *Edited by* N.V. DeByle and R.P. Winokur. USDA For. Ser. Gen. Tech. Rep. RM-119. pp.29-33.

Steneker, G.A. 1976. Guide to the silvicultural management of trembling aspen in the prairie provinces. Can. For. Serv. North. For. Cent. Inf. Rep. NOR-X-164.

Stoeckeler, J.H., and Macon, J.W. 1956. Regeneration of aspen cutover areas in northern Wisconsin. J. For. 54: 13-16.

Stone, D.M., and Elioff, J.D. 1998. Soil properties and aspen development five years after compaction and forest floor removal. Can. J. Soil Sci. 78: 51-58.

Tappeiner, J.C., and Alm, A.A. 1972. Effect of hazel on the nutrient composition of annual litter and forest floor in jack and red pine stands. Minnesota For. Res. Note. 235.

Tew, R.K. 1970. Root carbohydrate reserves in vegetative reproduction of aspen. For. Sci. 16(3): 318-320.

Winder, R.S., and Macey, D.E. 2001. The influence of edaphic and competitive factors on productivity of marsh reed grass (Calamagrostis Canadensis) in a cooperative pathosystem. Can. J. Bot. 79: 805-814.

Zehngraff, P.J. 1946. Season of cutting affects aspen sprouting. USDA For. Serv. Lake States For. Exp. Sta. Tech. Note 250.

Zehngraff, P.J. 1949. Aspen as a forest crop in the Lake States. J. For. 47: 555-565.

CHAPTER II

Aspen regeneration in relation to residual density and season of cut

Introduction

Aspen (*Populus tremuloides* Michx.) is a fast growing, shade intolerant, early successional tree species that regenerates primarily by vegetative propagation through root suckers from its extensive lateral root system (Day 1944, Farmer 1962, Lavertu et al., 1994, Frey et al 2003). Root sucker regeneration in aspen is linked to the disruption of apical dominance (Farmer 1962). The shallow lateral roots of aspen regenerate aggressively after above ground disturbance, such as fire or clearcutting, removes or kills the aboveground portion of the stand (Crouch 1981, DesRochers and Lieffers, 2001, Frey et al. 2003). The maintenance of apical dominance has been attributed to the group of plant hormones called auxins, which are produced in the swelling buds, growing shoots and leaves (Eliasson 1971, Frey et al. 2003). Removal of the apical dominance will stimulate root suckering through a change in the ratio of auxin:cyctokinins in the roots; auxins are produced in the shoots and are translocated to the roots and cytokinins are produced in the actively growing root tips. An increase in the proportion of cytokinins in the roots is thought to promote development of shoot buds on the roots (Farmer 1962, Eliasson 1971, Fitzgerald 1983, Frey et al. 2003).

The majority of regenerating root suckers are established within the first 2 years after disturbance and regenerating densities have been reported to range from 3,125 stems per hectare (sph) to over 100,000sph (Zehngraff 1946, Stoeckeler and Macon 1956, Jones and Trujillo 1975, Steneker 1976, Crouch 1986, Bates et al 1993). This prolific regeneration of aspen can pose a competitive threat to white spruce (*Picea glauca* Moench Voss) seedlings, commonly growing together with aspen in boreal mixedwood stands. In order to promote the slower growing white spruce in mixedwood stands, forest managers attempt to reduce the amount of aspen regeneration (Day, 1944).

It is generally accepted that clearcutting of aspen (removal of all stems) stimulates the most suckering and is the recommended silvicultural system to promote regeneration

of aspen (Farmer 1962, Doucet 1989, Bates et al. 1993, Frey et al. 2003). Maintaining a partial aspen residual canopy typically results in reduced regeneration; through either shade or hormonal suppression by the residual aspen ramets (Stoeckeler and Macon 1956, Schier and Smith 1979, Crouch 1983, Bella 1986, Bates et al. 1993, Huffman et al. 1999). Therefore, when aspen is grown in association with white spruce, maintaining a partial overstory of aspen might be used to reduce the level of sucker regeneration and still provide sufficient light for reasonable growth of white spruce (Day 1944, Bell et al. 1997, Comeau et al. 1998, Bell et al. 1999). Similar with thinning paper birch (Betula *papyrifera* Marsh.), Comeau et al. (1998) found that regenerating birch densities were reduced when a birch residual overstory was retained in 33-year-old birch stands. Leaving residual aspen stems in 10-year-old regenerating mixedwood stands might provide sufficient levels of auxins to the root systems to greatly reduce the suckering response since many of the young stems are interconnected either clonally or through root grafts (Mowrer 1988, DesRochers and Lieffers 2001). Leaving part of the aspen canopy on a site might also reduce the growth of newly initiated suckers due to increased shade. Johansson (1986) concluded with birch stump sprouts low light intensities may contribute to reduced growth and inhibition of sucker development.

Harvesting in mature stands at different times through the season has been found to have an impact on regeneration densities in mature stands (Zehngraff 1946, Stoeckeler 1947, Farmer 1962, Bates et al. 1993). These differences are thought to be related to seasonal changes in carbohydrate reserves and plant hormones. Aspen root carbohydrate reserves were found to be lowest in the winter and spring and higher during the summer months (Landhäusser and Lieffers 2003). But others (Farmer 1962, Tew 1970, Eliasson 1971, Schier and Zasada 1973, Bell et al. 1999) suggest that suckering is influenced more by apical dominance regardless of season. However, carbohydrate reserves might play an important role in the rate of growth of suckers (Farmer 1962, Frey et al. 2003). Height growth and leaf area development of suckers has been related to root carbohydrate reserves (Schier and Zasada 1973, Landhäusser and Lieffers 2002). Studies with birch have show that that low levels of starch found in roots were associated with fewer shorter sprouts being produced off the connected cut stem.

The objectives of this study were to examine the rates of re-suckering and resprouting of juvenile (10-year-old) aspen stands that were thinned to three different residual densities at three different phenological stages. In addition the seasonal changes of root carbohydrates reserves were assessed over a full growing season after cutting and related to the cutting and residual density treatments.

Methods and Materials

Two study areas were selected for the experiment. One was located approximately 50km North East of Lac La Biche, Alberta (54° 58′ N, 111° 59′ W), in the Boreal Mixedwood ecological region. Plots were located on fine textured Gray luvisolic soils. The general elevation was 585 m above sea level. The total annual precipitation was 533.3 mm in 2003 and 516.5 mm in 2004. Stands in Lac La Biche were composed of trembling aspen (average density 17,000sph) with a minor component of balsam poplar (*Populus balsamifera* L.) and paper birch (*Betula papyrifera* Marsh.). The important shrubs were beaked hazelnut (*Corylus cornuta* Marsh), willow (*Salix* sp.), and choke cherry (*Prunus virginiana* L.), wild rose (*Rosa acicularis* Lindl.) and Marshreed grass (*Calamagrostis canadensis* Michx.) dominated below the shrubs.

The second research site was located about 45 km North West of Peace River, Alberta, (56° 24′ N, 117° 47′ W) in the Boreal Mixedwood ecological region. Similarly to the Lac La Biche sites, the dominant soil type was a gray luvisol. The elevation is 762 m above sea level. Total annual precipitation in Peace River was 363.5 mm for 2003 and 521.3 mm in 2004. Species composition of the stands in the Peace River site were trembling aspen (average density 23,000 sph), with a minor component of balsam poplar, paper birch. Green alder (*Alnus crispa* (Ait) Turrill) was the dominant shrub, with some willow, wild rose and marsh reed grass.

Five juvenile aspen stands, regenerated after clearcut harvesting were selected in the Lac La Biche area and four stands in the Peace River area after one site was removed from aspen measurements because the size of the aspen was much greater than the other nine sites. Stand age varied between 9 and 10 years. Stands were on average 20 ha and had at least 85% aspen stems with the remainder made up of balsam poplar and birch.

Within each of the nine stands, ten plots (50 x 50 m) of uniform tree size and stem density were located. At each plot center one tree was flagged and its location was recorded by Garmin GPS 12 Personal Navigator unit. We chose this large plot size to minimize the clonal effect of edge trees in the plot center. All measurements occurred within a 5 m radius from plot center. The plot center tree was included as one of the residual trees in the residual density treatments. In the clearcut treatments the plot center tree was cut about 1 m above the ground.

Three times of thinning (summer, winter and spring) and three different residual target densities (0, 500, and 1,500 stems per hectare (sph)) were applied. The three cutting times were based on three different phenological stages of aspen stands; the first thinning occurred in late summer (August 13-25, 2003) after termination of shoot growth but with leaves still green. The second thinning occurred when trees were still in winter dormancy (April 12-24, 2004 – spring was late, as air temperatures were low and the ground was still frozen and the sites covered with snow). The third thinning was in the spring immediately after bud flush (May 27 through June 4, 2004). The three residual densities and times of thinning were randomly assigned to nine plots on each block, in addition, one control plot was established which received no thinning treatment. Therefore each block consisted of ten plots with nine treatment combinations and a control. Three workers cut the trees and shrubs leaving a dominant tree every 4.5m for a total of 500sph or every 2.5m for 1,500sph treatment density to achieve the desired residual treatment densities. To ensure consistent residual densities, leave trees were selected and marked on a grid around plot center for the 500 and 1,500sph treatment plots. All trees were cut in the complete removal treatment plots. For each treatment, trees and all the shrubs were cut at a 15cm height and slash remained on site. For each of the three treatment times the manual thinning treatments occurred first in Lac La Biche followed by Peace River.

Pre-treatment Measurements

In each plot three circular sub-plots (1.78 m in radius) were used to measure initial conditions of the plots. Sub-plots were located 3 m from plot center at 360, 120, and 240 degrees. Diameters at breast height were recorded for each aspen or balsam

poplar tree present in the sub-plots. One tree, of the average canopy height was measured in each sub-plot to obtain an average height for the plot. Since there was a high incidence of green alder in the Peace River sites, beaked hazelnut in the Lac La Biche sites and willow in both sites, the number of alder, hazel, and willow stems was also recorded in the sub-plots. Percent grass cover was estimated for each of the sub-plots.

Post treatment measurements

Aspen and shrub regeneration was measured in late August and early September 2004 using the same sub-plots as used for the initial measurements. No regeneration was produced before the end of the growing season after the summer cuts. Regeneration of aspen was identified as either suckers (sprouting from the root system) or sprouts (sprouting from the cut stems). When multiple suckers or sprouts originated from an area of less than 12 × 12 cm, or were centered on a central cut stem, this group of stems was defined as a cluster. In this cluster the height of only the tallest shoot was measured from the ground and the total number of sprouts or suckers in the clusters was recorded. Height was measured for a minimum of 10 sprouts or suckers in each subplot. The plots were sub divided into quadrants and quadrants were added until at least 10 sprouts or suckers were measured. Leaves of all measured sprouts or suckers were collected to determine leaf mass and sub-samples were used to calculate specific leaf area in order to develop the leaf area index (m^2 of leaf area per m^2 of ground area) for each treatment. The total number of re-sprouted stems from cut shrub stumps was counted throughout the entire sub-plot and the height of the tallest re-sprout was measured. Post treatment percent grass cover was estimated.

Root Carbohydrates

In the five Lac La Biche stands, aspen root samples (0.5-1.0 cm in diameter) were collected from the residual trees and from suckering roots or sprouting stems for non-structural carbohydrate analysis. Samples were collected outside the plot center to minimize the impact on regeneration. Five collections were made: in September 2003 one month after the late summer thinning; during winter dormancy which coincided with the thinning in April 2004; after spring flush in late in late May 2004; the following

growing season (July 2004); and the last collection after the growing season in September 2004. Root collection in Peace River was limited to the control plots. This sampling was to verify that the sites had similar seasonal changes in carbohydrate reserves as the Lac La Biche control plots.

Root samples were kept chilled until they came to the lab for carbohydrate analysis. Samples were oven dried at 68 °C and ground to pass a 40-mesh screen of a Wiley mill. Soluble sugars were extracted from ground tissues by boiling samples three times with 80 % hot ethanol at 95 °C. Phenol-sulfuric acid was used to analyze the ethanol extract for total sugar concentrations. Starch was digested using an enzyme mixture of α-amylase and amyloglucosidase followed by the colorimetric measurement of the glucose hydrolysate using a peroxidase-glucose oxidase-o-dianisidine reagent (Chow and Landhäusser 2004).

Experimental design and statistical analysis

There were no significant interactions for any of the response variables related to aspen or shrub regeneration for the two stand locations, (Peace River and Lac La Biche), so site location was not considered a factor in the analysis. Aspen regeneration densities, height and leaf area were analyzed as a factorial experiment with a randomized complete block design with three levels of residual stem density and three times of thinning. One-way ANOVA was used to explore differences in the seasonal root carbohydrate concentrations.

Analysis of alder response to cutting was limited to three stands in Peace River that had a large enough component of the species. Hazel response to cutting was also limited to three stands in the Lac La Biche area that had a high enough component of hazel to be used for analysis. For willow and grass cover, all 10 stands were used in the analysis. Data for alder, hazel, willow and *Calamagrostis canadensis* grass were also analyzed as a randomized complete block design, 2-way factorial treatment structure.

Results

Since there were no significant interactions between the times of thinning and the residual density treatments for all measured aspen regeneration variables (density, height, leaf area index or root carbohydrates), the timing and residual density treatments were interpreted separately. For additional information, means for the response variables of all treatment combinations are presented in Appendices A and B.

Residual aspen density treatment

Aspen densities prior to treatment averaged 21,000 sph. Residual aspen density had a significant effect on the total number of regenerating sprouts and suckers ($P=<0.0001$); however, by the end of the first full growing season the number of stump sprouts and suckers combined for each residual density treatment was more than three times greater than stems prior to treatment (Fig. 2.1). On average 91 % of the regenerating stems were stump sprouts.

Although the number of sprouts and suckers were high there was a decline in number of regenerating stems when residual aspen stems were maintained on the plots ($P=<0.001$). The complete clearing treatment regenerated to 91,000 sph (Fig. 2.1a.), compared to 70,000 sph when 500 sph residuals were left and 56,000 sph for the 1,500 sph residuals. However, if sprouts and suckers were counted in clusters, which will likely self thin to 1 stem in the future, the amount of regeneration was significantly reduced to 26,000 sph in the complete clearing treatment, to 20,000 sph in the 500 sph treatments and 18,000 sph in the 1500 sph treatment plots. These values did not differ from their initial densities.

Height of regenerating stems was significantly greater in the complete clearing treatment (82.8 cm) compared to both residual treatments (67.5 cm, Fig. 2.1b.). Regenerating stems in the complete clearing treatment produced a significantly greater leaf area index, 0.7 than regeneration in the 500 sph (LAI = 0.3) and 1,500 sph residual treatments, (LAI = 0.3) ($P=<0.001$, Fig. 2.1c.), however, the leaf area index for the 500 and 1500 sph treatments were not significantly different.

Time of thinning

The time of thinning had no effect on the number of regenerating stems P=0.5540 (Fig. 2.2a) and there was no significant effect of time of thinning on the number of stump sprouts (P=0.3302), suckers (P=0.1951), or leaf area index (P=0.0774).

First year height growth of the regeneration in the spring thinning treatment, 64.0 cm (Fig. 2.2b), was significantly less than at the two other thinning times, where height growth was 74.0 cm in the summer thinning and 80.0 cm in the winter; these two treatments were not significantly different from each other.

Root Carbohydrates

Seasonal root carbohydrates were analyzed from Lac La Biche sites. Control sites in the Peace River and Lac La Biche sites showed similar seasonal patterns and therefore we assume that the response of carbohydrate reserves of the residual trees and regeneration of the treatments in Peace River will likely be similar.

Effects of residual density on root carbohydrate reserves

Sugar

Throughout the collection period the sugar concentrations of roots of residual trees (regardless of residual density) generally changed similarly to the unthinned control trees (Fig 2.3a.). However in the complete clearing, roots collected in September 2003 emanating from stumps had sugar concentrations of 13 %, which was significantly higher than the roots connected to controls (9 %). By the end of the first growing season in 2004, sugar levels declined in roots attached to residual trees while sugar concentrations were higher in roots associated with regenerating stems, especially in the completely cleared treatment. In September 2004, there is a trend of decreasing sugar concentrations in roots from regenerating stems associated with increasing residual stems. I observed 11 % sugar dry weight in the regenerating roots in the complete clearing treatment, 10 % with 500 sph residual trees and 9 % with 1,500 sph of residual trees.

Starch

In September 2003, sites cut in August had lower root starch concentrations than the controls (Fig 2.3b.). There was 12.2 % starch dry weight in the controls trees followed by 8.8 % in the 1,500 sph residual treatment, 6.4 % in the 500 sph treatment and 5.6 % in roots from stumps in the complete clearing treatment. By the following spring these differences in root starch concentrations in the residual trees were not detectable.

After resprouting and suckering in July 2004, roots associated with the regeneration from the three residual treatments had 1 % starch concentration, which was significantly less than in roots associate with residual trees and control trees (9 %). From July to September starch levels increased sharply in roots associated with regenerating sprouts, but starch concentrations still remained significantly lower than in the roots associated with residual stems or control plots. In addition, as the number of residual trees increased, the starch concentration decreased in the roots associated with regenerating sprouts, although the differences were not significant: 10 % dry weight in the complete clearing treatment, 9 % in the 500 sph residual treatment and 7 % in the 1,500 sph treatment.

Total non-structural carbohydrates (TNC)

Overall, root TNC concentrations followed a similar seasonal pattern to root starch concentrations. In July 2004, the roots associated with sucker or sprout regeneration in all residual treatments had 9 % TNC which was half the concentration determined in roots associated with the residual and control trees 18 % (Fig 2.3c.). By September 2004 roots associated with regeneration had reached an average TNC concentration of 19 % and were similar to the roots associated with residual trees (average 22 %). However, regenerating roots in the 1,500 sph residual treatment still had significantly lower TNC levels (16 %) than roots associated with residual and control trees.

Effects of time of thinning on root carbohydrate reserves

Sugar

In September 2003, sugar concentrations (11 %) in roots associated with residual trees in the plots that were thinned in the summer were significantly higher than sugar concentrations of roots in the control plots (9 %); by the spring of 2004 these differences have disappeared (Fig. 2.4a.). By September 2004 sugar concentrations of roots associated with regeneration were 10 %. This value was significantly higher than found in the roots of residual trees (8 %).

Starch

In September 2003, roots of the controls had nearly double the starch concentration (12 %), of roots from residuals in the summer thinning treatments (7 %, Fig. 2.4b.). However from April to September 2004, these differences were no longer significant. In July 2004, starch concentrations of roots associated with regeneration had significantly lower starch concentrations (1 %) regardless of time of thinning than roots associated with residual trees (average 9 %). By September 2004, starch concentrations of regenerating roots increase to an average of 9 % while residual and control tree roots had an average concentration of 14 %. However, starch in roots associated with regeneration from the winter thinning recovered to levels that were not significantly different than starch found in residual roots from the spring and summer thinnings.

Total non-structural carbohydrates (TNC)

In September 2003 root TNC concentrations from residual trees was 18%, which was significantly lower than the 22% root TNC of the control trees (Fig. 2.4c.). In July 2004, the average TNC concentrations of roots of regenerating sprouts was 9.0 %, which was significantly less than the average TNC concentrations of roots from residual tree and the control trees, 18.1 %. By the September 2004, TNC concentrations from roots of regenerating trees recovered to levels similar to the roots of residual and control tree. When comparing roots from regeneration, the winter thinning treatments had greater TNC concentration than thinnings done in the spring and summer.

Shrubs

There was little difference in alder, beaked hazel or willow density (Table 2.1) or height (Table 2.2) in relation to season of thinning or density of residual aspen. Similarly, the grass cover was not related to treatment. However, there was an overall reduction in the percent grass cover after treatment likely due to the amount of slash (Table 2.1). Observations from the following growing season, however, show the grass was back to the cover found in the control plots.

Discussion

Residual aspen density treatment

Retaining residual trees did lead to a significant reduction in the number of regenerating stems one year after cutting juvenile stands of aspen, relative to cutting all of the stems (Fig. 2.1). There was also a decline in leaf area index in the stands with increasing amounts of residual stems. This was similar to findings of Huffman et al. (1999) who found that residual trees tended to decrease the density of regenerating stems. In our study, however, there was a significant decline in height of regeneration from plots with residuals relative to completely cleared plots; Huffman et al. (1999), however, did not see a similar decline in height. Overall, however, none of the cutting treatments in the juvenile phase, involving either complete clearing or partial cutting, will likely be effective at maintaining lower densities of regenerating aspen, as even the lowest treatment produce more than 50,000 sph.

An explanation for why regeneration so greatly exceeded pretreatment densities is that there was a clustering of regeneration, i.e. multiple stems regenerating off one individual stump or a small section of the root system. Clusters of greater than ten individual stems in a small area inflated the number of stems. Others (Crouch 1986, Mowrer 1988, Doucet 1989, Huffman 1999, Frey et al 2003) have reported large reductions in the number of aspen stems after 5 and 10 years of growth, mostly due to self-thinning of these clusters. Jones (1975) observed 38% mortality after 4 years and this was expected to reach 90% mortality by 10 years (Jones 1975, Schier et al. 1985).

Therefore, based upon our analysis of clustering regeneration (Fig. 2.1), the rapid initiation of stems, and presumably the shading leaf area that goes with them, will quickly return the stands to pre-treatment conditions.

We saw an effect of residual density on root carbohydrate reserves. First, by September 2003, a month after the summer cut, the roots in the cut stands had lower TNC reserves than the control (Fig. 2.3). This is expected, as the cut stands would have had nearly one month less time to photosynthesize and build carbohydrate reserves later in the summer. It is noteworthy however, that by late winter there was no difference in TNC. Landhausser and Lieffers (2003) also found that TNC reserves in roots were greatly reduce by spring, perhaps related to a pulse of root growth in fall. The carbohydrate reserves of the roots associated with developing sprouts and suckers in July 2004 was much lower than the roots adjacent to residual trees or in the control plots. This was likely related to the use of carbohydrates to build regenerating stems. By September of 2004, however, roots in the complete clearing treatment were able to accumulate a greater amount of carbohydrates (starch and TNC) than the roots associated with suckers in the stands with residual trees. Presumably, this is related to increased shading of suckers from residual trees, which can hamper sucker growth rates after emergence (Bates et al. 1989). Another contributor to the higher reserves in the completely cleared treatment could be from the greater leaf area development in the complete clearing regeneration, which is critical for re-building carbohydrate reserves (Landhäusser and Lieffers, 2002).

It is noteworthy that most of regenerating stems were from stump sprouts and not from root suckers. This is the reverse of what would be seen in mature stands where virtually all regenerating stems come from root suckers (Frey et al. 2003). The implications of increased levels of stump sprouts compared to suckers are that there is likely to be increased decay of stems emanating from stumps than from suckers. This may have negative implications for wood quality for mixedwood stands given an early thinning treatment.

Time of thinning

The seasonal time of thinning made no significant difference a regenerating density after one growing season. To our knowledge this is the first study of the effect of timing of thinning on suckering response of juvenile stands, but there are have been several studies with conflicting results in regards to timing of clearcutting mature stands. Similar to our study, Bell et al. (1999) found no effect of season of cutting on regenerating density. In contrast, Baker (1918) and Zehngraff (1946, 1949) found the least suckers after cutting in early summer while Bella (1986) found the best regeneration after cutting in summer; Bates et al. (1993) noted numbers of suckers increase after cuts late in the growing season. Eliasson (1971) found the capacity of excised sections of root to initiate suckers to be at a minimum in June and he speculated that this is likely from reductions in carbohydrate reserves during this season. However, it is generally accepted that the vigour but not the number of suckers initiated is dependent on the amount of stored root carbohydrates (Schier and Zasada 1972, Frey et al., 2003) and therefore seasonal fluctuations in carbohydrates should play a minimal role in the density of regeneration produced.

Season of cutting did however influence height growth in the regenerating stand; with cutting in winter resulting in the tallest suckers. Carbohydrates tended to be slightly higher for roots associated with residual trees for plots cut in winter throughout the 2004 growing season. Further, the TNC reserves associated with roots connected to regenerating stems cut in winter had carbohydrate reserves that were similar to the roots of residual stems by September 2004. Presumably this was related to the tendency for larger numbers of suckers and greater development of leaf area in the plots cut in winter. Root TNC concentrations were lowest at the time of spring thinning and resulted in regeneration with the smallest height growth and leaf area development. Landhäusser and Lieffers (2002) also observed poor growth after spring cuts. This poor growth could be attributed to depleted carbohydrate reserves by leaf flush.

Our results suggest that cutting at different phenological stages when roots are at low or high points in their annual cycle of carbohydrate reserves plays little role in determining the number of regenerating stems. As suggested by other studies complete

release of apical dominance by complete clearing is the most important factor stimulating numbers of suckers. While there have been ample studies that reported that carbohydrate levels are important in influencing sucker growth and survival (Farmer 1962, Schier and Zasada 1972, Schier, Jones and Winokur 1985, Bell et al. 1999), the results were not that clear in our study. The best growth of suckers occurred after the winter thinning, but the highest levels of root TNC were actually at the time of the late summer cut (Fig. 2.4c). This suggests that factors other than TNC reserves limited the growth of regeneration in the summer thinning.

Shrubs

Similar to aspen, alder, hazel and willow re-sprouted in clumps so densities will likely be reduced in the future. However, there is high variability in the results of the shrub analysis because of a low sample size. Overall, grass cover was reduced the following growing season likely due to slash however observations in the second growing season following treatment indicate a recovery in grass cover.

Table 2.1. Stem density of shrubs, pre-thinning (Pre-) and post thinning (Post) of the aspen overstory, after the first growing season, in relation to density of residual aspen trees and season of thinning; alder (n=9), hazel(n=9) and willow (n=30) and percent grass cover (*Calamagrostis canadensis*) (n=30). Treatment means with the same letter in columns and within the residual density and time of thinning treatments are not significantly different.

	Alder		Hazel		Willow		Grass (% cover)	
Residual density	Pre-	Post	Pre-	Post	Pre-	Post	Pre-	Post
0	18 333[a]	11741[a]	13259[a]	18667[a]	5750[a]	31597[a]	17[a]	8[a]
500	9666[a]	11815[a]	10925[a]	7000[a]	10004[a]	18233[a]	15[a]	9[a]
1500	16519[a]	12482[a]	5556[a]	21778[a]	5798[a]	21483[a]	23[a]	8[a]
Time of thinning								
summer	5111[a]	8741[a]	2518[a]	17926[a]	7833[a]	32119[a]	16[a]	9[a]
winter	20519[a]	12259[a]	21185[a]	18852[a]	8014[a]	18511[a]	21[a]	9[a]
spring	18889[a]	15037[a]	6037[a]	10666[a]	5704[a]	20683[a]	18[a]	7[a]

Table 2.2. Height of shrubs after the first growing seasoning after thinning; alder (n=9), hazel (n=9) and willow (n=30) and percent grass (*Calamagrostis canadensis*) cover (n=30). Treatment means with the same letter in columns and within the residual density and time of thinning treatments are not significantly different.

	Height (cm)			Percent Cover
Residual density	alder	hazel	willow	grass
0	51.14[a]	54.647[ab]	129.69[a]	8[a]
500	58.93[a]	42.416[b]	110.85[a]	9[a]
1500	49.86[a]	64.087[a]	107.41[a]	8[a]
Time of thinning				
summer	58.35[a]	60.246[a]	134.37[a]	9[a]
winter	61.10[a]	50.799[a]	113.05[a]	9[a]
spring	40.47[a]	50.105[a]	100.54[a]	7[a]

Figure 2.1. Effects of residual density of aspen on aspen regeneration one year after thinning A. Density of regeneration as the proportion of stump sprouts and suckers presented as the total number of stems and total number of clusters. Different letters over the bar indicate significant differences in the sum of stump sprout and sucker densities determined for the total number of stems and clusters. Total stem and cluster density were analyzed separately (n=27); B. Height of regenerating stems (summing suckers and stump sprouts) (n=27); and C. Leaf area index of regenerating stems (summing stump sprouts and suckers) (n=27). Means with the same letter are not significantly different.

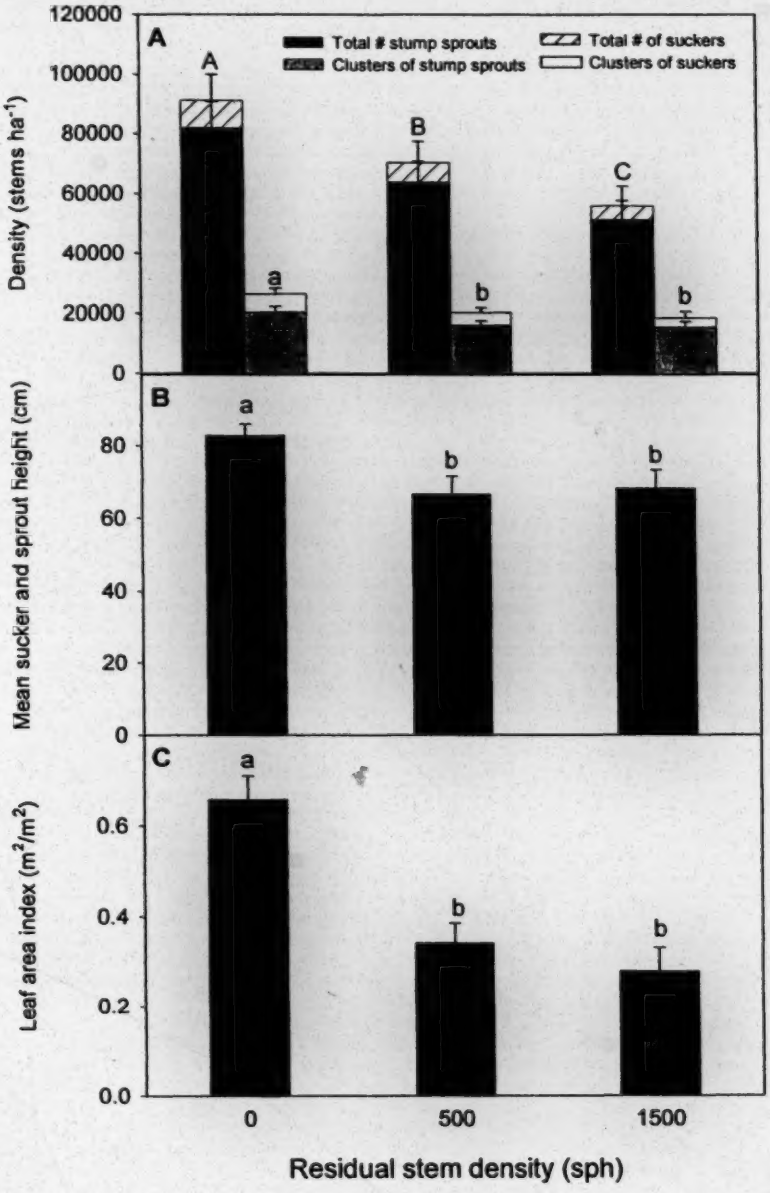


Figure 2.2. Effects of time of thinning on aspen regeneration one year after thinning A. Density of regeneration as the proportion of stump sprouts and suckers for the total number of stems and the total number of clusters. Different letters over the bar indicate significant differences in the sum of stump sprout and sucker densities determined for the total number of stems and clusters. Total stem and cluster density were analyzed separately (n=27); B. Height of regenerating stems (summing suckers and stump sprouts) (n=27); and C. Leaf area index of regenerating stems (summing stump sprouts and suckers (n=27). Means with the same letter are not significantly different.

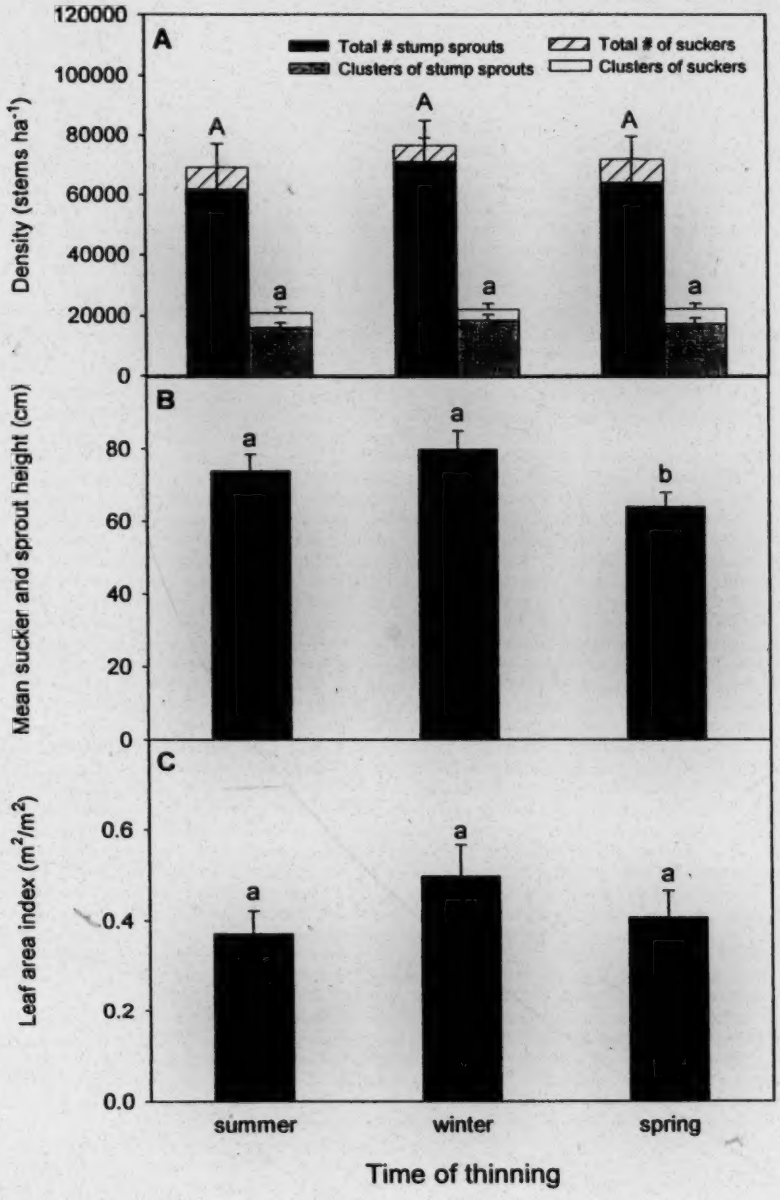


Figure 2.3. Effects of residual density treatment on carbohydrate concentrations in roots associated with residual trees (-r) and from roots associated with regenerating sprouts (-s) after regeneration started in July. A. sugars, B. starch and C. total nonstructural carbohydrates. Collections from roots emanating from residual trees started in September 2003. Collections from roots associated with sprouts were collected in July and September 2004 in the first year after thinning. For September 2003 and April 2004 n=5, for May 2004 n=10, for July and September 2004 n=15.

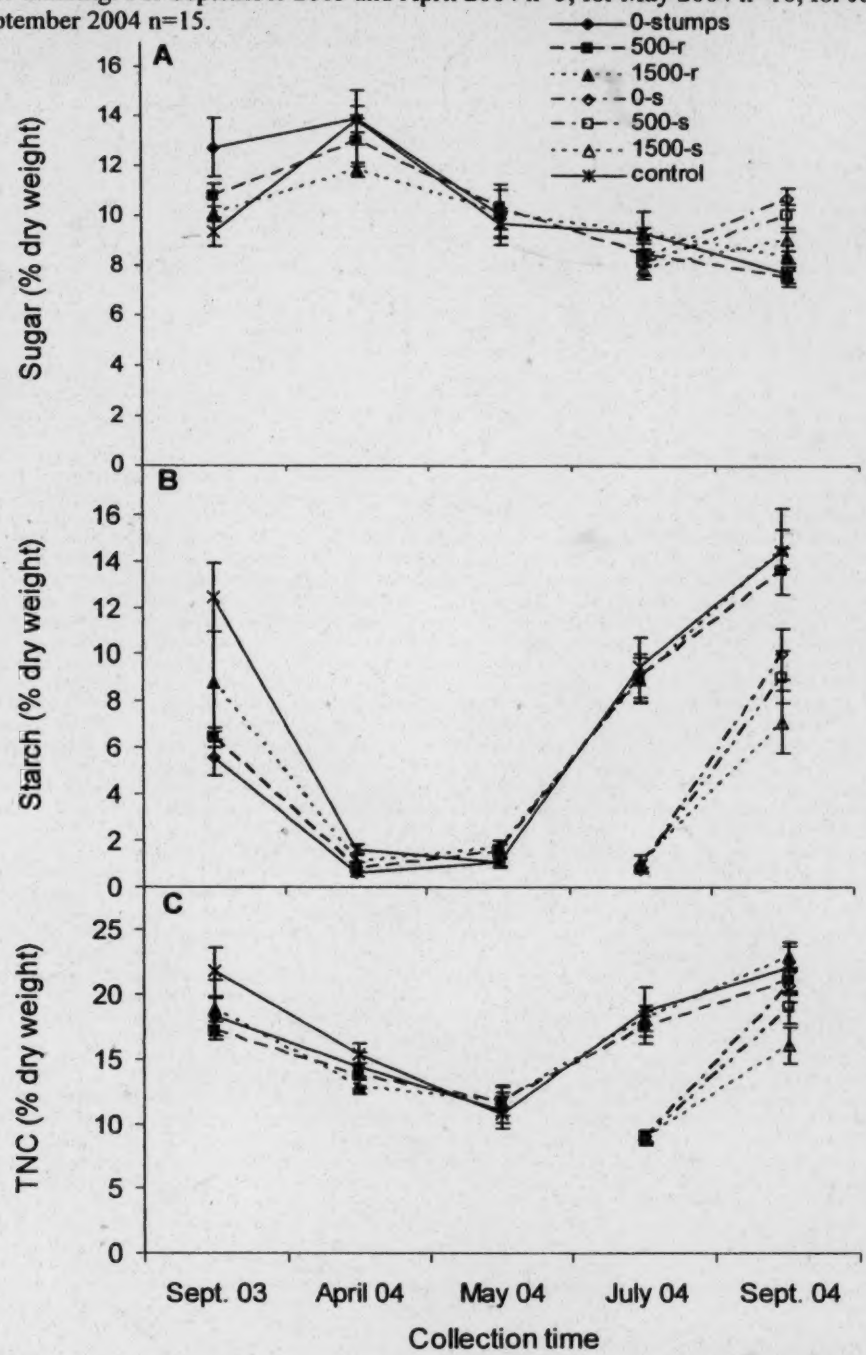
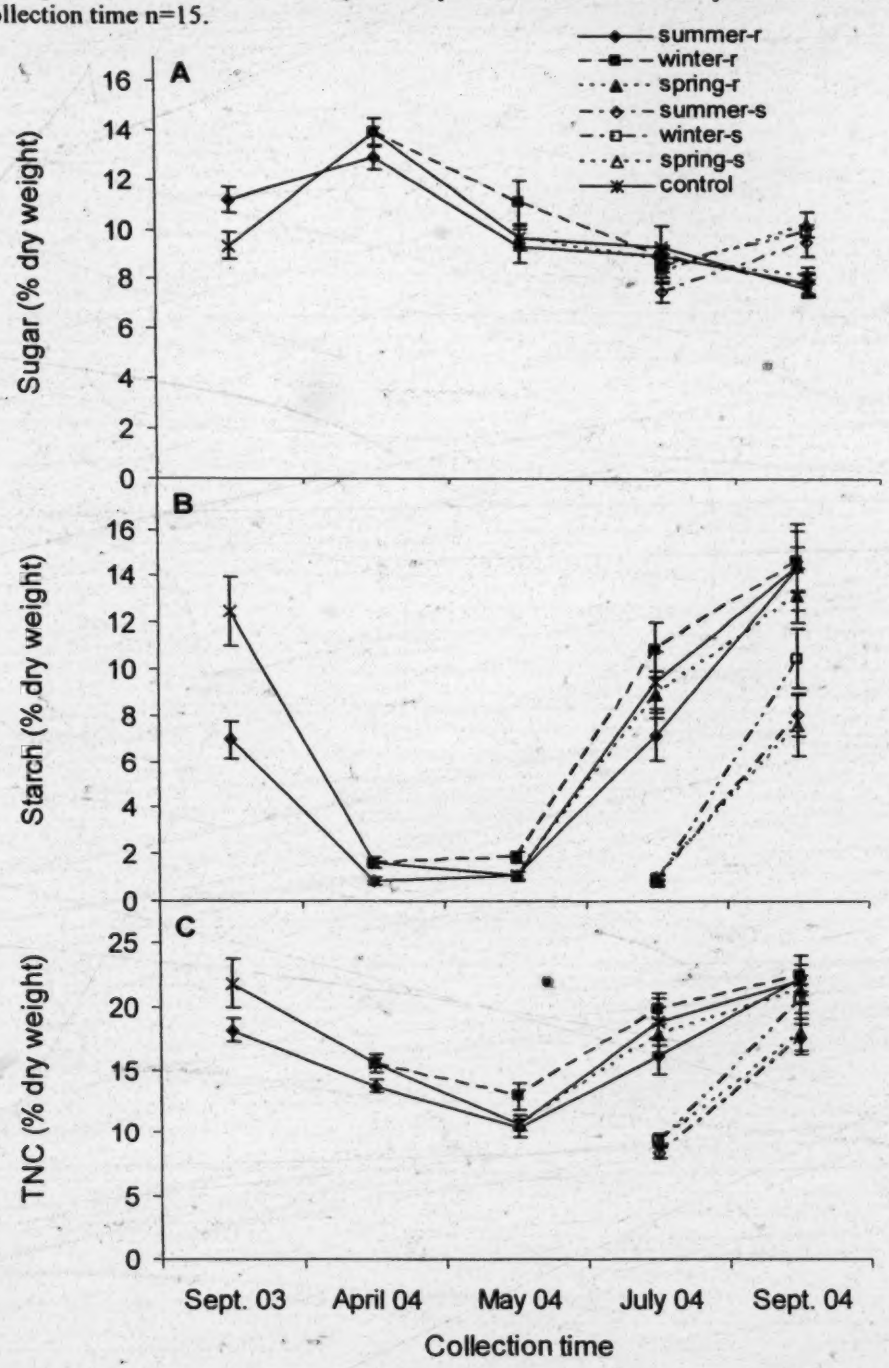


Figure 2.4. Effects of time of thinning on carbohydrate concentrations in roots associated with residual trees (-r) and from roots associated with regenerating sprouts (-s) after regeneration started in July. A. sugars, B. starch and C. total nonstructural carbohydrates. Collections from roots emanating from residual trees started in September 2003. Collections from roots associated with sprouts were collected in July and September 2004 in the first year after thinning. For each collection time n=15.



References

Baker, F.S. 1918. Aspen reproduction in relation to management. J. For. 16: 389-398.

Bates, P.C., Blinn, C.R., and Alm, A.A. 1993. Harvesting impacts on quaking aspen regeneration in northern Minnesota. Can. J. For. Res. 23: 2403-2412.

Bates, P.C., Blinn, C.R., Alm, A.A., and Perala, D.A. 1989. Aspen stand development following harvest in the Lake States Region. North. J. Appl. For. 6: 178-183.

Bell, F.W., Pitt, D.G., Morneault, A.E., and Pickering, S.M. 1999. Response of immature trembling aspen to season and height of cut. North. J. Appl. For. 16(2): 108-114.

Bell, F.W., Lautenschlager, R.A., Wagner, R.G., Pitt, D.G., Hawkins, J.W., and Ride, K.R. 1997. Motor-manual, mechanical, and herbicide release affect early successional vegetation in northwestern Ontario. For. Chron. 73(1): 61-68.

Bella, I.E. 1986. Logging practices and subsequent development of aspen stands in east-central Saskatchewan. For. Chron. 62: 81-83.

Chow, P.S., and Landhäusser, S.M. 2004. A method for routine measurements of total sugar and starch content in woody plant tissues. Tree Phys. 24: 1129-1136.

Comeau, P.G., Wang, J.R., Letchford, T., and Coopersmith, D. 1998. Effects of birch spacing on birch resprouting and understory light. In: Third International Conferrence of Forest Vegetation Management; Popular Summaries, R.G. Wagner and D.G. Thompson (comp.). Ont. Min. Nat. Resour., Ont. For. Inst., For. Res. Info. Pap. No. 141. pp. 78-80.

Crouch, G.L. 1981. Regeneration on aspen clearcuts in northwestern Colorado. USDA For. Serv. Res. Note RM-407.

Crouch, G.L. 1983. Aspen regeneration after commercial clearcutting in southwestern Colorado. J. For. 81: 316-319.

Crouch, G.L. 1986. Aspen regeneration in 6- to 10-year-old clearcuts in southwestern Colorado. USDA For. Serv. Res. Note RM-467.

Day, M.W. 1944. The root system of aspen. Am. Midl. Nat. 32:502-509.

DesRochers, A., and Lieffers, V.J. 2001. Root biomass of regenerating aspen (*Populus tremuloides*) stands of different densities in Alberta. Can. J. For. Res. 31: 1012-1018.

Doucet, R.1989. Regeneration silviculture of aspen. For. Chron. 65: 23-27.

Eliasson, L. 1971. Growth regulators in *Populus tremula* III. Variation of auxin and inhibitor level in roots in relation to root sucker formation. Physiol. Plant. 25: 118-121.

Farmer, R.E. 1962. Aspen root sucker formation and apical dominance. For. Sci. 8: 403-410.

Fitzgerald, R.D., and Hoddinott, J. 1983. The utilization of carbohydrates in aspen roots following partial or complete top removal. Can. J. For. Res. 13: 685-689.

Frey, B.R., Lieffers, V.J., Landhäusser, S.M., Comeau, P.G., and Greenway, K.J. 2003. An analysis of sucker regeneration of trembling aspen. Can. J. For. Res. 33: 1169-1179.

Huffman, R.D., Fajvan. M.A., and Wood, P.B. 1999. Effects of residual overstory on aspen development in Minnesota. Can. J. For. Res. 29: 284-289.

Johansson, T. 1986. Development of suckers bt two-year-old birch (Betula pendula Roth) at different temperatures and light intensities. Scand. J. For. Res. 1:17-26.

Jones, J.R. 1975. Regeneration on an aspen clearcut in Arizona. USDA For. Serv. Res. Note RM-285.

Jones, J.R., and Trujillo, D.P. 1975. Development of some young aspen stands in Arizona. USDA For. Serv. Res. Pap. RM-151.

Jones, J.R., and Winokur 1985

Landhäusser, S.M., and Lieffers, V.J. 2002. Leaf area renewal, root retention and carbohydrate reserves in clonal tree species following above-ground disturbance. J. Ecol. 90: 658-665.

Landhäusser, S.M., and Lieffers, V.L. 2003. Seasonal changes in carbohydrate reserves in mature northern *Populus tremuloides* clones. Trees 17: 471-476

Lavertu, D., Mauffette, Y., and Bergeron, Y. 1994. Effects of stand age and litter removal on the regeneration of *Populus tremuloides*. J. Veg. Sci. 5: 561-568.

Mowrer, H.T. 1988. Is managing aspen density worthwhile? In: Proceedings – Future Forests of the Mountain West: A stand culture symposium. W.C. Schmidt (compiler). USDA For. Serv. Gen. Tech. Rep. INT-243. pp. 201-209.

Schier, G.A., and Zasada, J.C. 1973. Role of carbohydrate reserves in the development of root suckers in *Populus tremuloides*. Can. J. For.Res. 3: 243-250.

Schier, G.A., and Smith, A.D. 1979. Sucker regeneration in Utah aspen clone after clearcutting, partial cutting, scarification, and girdling. USDA For. Serv. Res. Note INT-253.

Schier, G.A., Jones, J.R., and Winokur, R.P. 1985. Vegetative regeneration. *In* Aspen: ecology and management in the western United States. *Edited by* N.V. DeByle and R.P. Winokur. USDA For. Ser. Gen. Tech. Rep. RM-119. pp.29-33.

Steneker, G.A. 1976. Guide to the silvicultural management of trembling aspen in the prairie provinces. Can. For. Serv. North. For. Cent. Inf. Rep. NOR-X-164.

Stoeckeler, J.H. 1947. When is plantation release most effective? J. For. 45: 265-271.

Stoeckeler, J.H., and Macon, J.W. 1956. Regeneration of aspen cutover areas in northern Wisconsin. J. For. 54: 13-16.

Tew, R.K. 1970. Root carbohydrate reserves in vegetative reproduction of aspen. For. Sci. 16(3): 318-320.

Zehngraff, P.J. 1946. Season of cutting affects aspen sprouting. USDA For. Serv. Lake States For. Exp. Sta. Tech. Note 250.

Zehngraff, P.J. 1949. Aspen as a forest crop in the Lake States. J. For. 47: 555-565.

CHAPTER III

Effects of *Calamagrostis canadensis* and *Corylus cornuta* on Trembling Aspen (*Populus tremuloides* Michx.) suckering.

Introduction

Trembling aspen (*Populus tremuloides* Michx.) is known to regenerate aggressively and densities can exceed 100,000 stems per hectare (Zehngraff 1946, Stoeckeler and Macon 1956, Jones and Trujillo 1975, Steneker 1976, Crouch 1986, Bates et al. 1993) is common after a disturbance removes the aboveground biomass. Root suckers are initiated from an extensive network of lateral roots within the upper 20 cm of the soil profile (Day 1944, Frey et al. 2003, Powell and Bork 2004a) and is the main means of regeneration of aspen. Linked to apical dominance, there is a tendency for a higher density of suckering with complete removal of the aspen canopy (Farmer 1962, Doucet 1989, Bates et al. 1993, Frey et al. 2003). However, complete removal alone will not guarantee a high regeneration density; there are other factors that need consideration. In many circumstances there is reduced regeneration of aspen in stands where there is a significant component of *Calamagrostis canadensis* Michx. or *Corylus cornuta* Marsh (beaked hazelnut) in the understory prior to disturbance. In the case of *C. canadensis*, there is considerable evidence that the litter of this grass insulates the soil and thereby delays soil thawing in spring (Hogg and Lieffers 1991, Landhäusser and Lieffers, 1998). Cool soils are known to reduce the growth of aspen seedlings (Landhäusser and Lieffers 1998) and cool soils associated with this grass are known to delay aspen regeneration (Fraser et al. 2002, Frey et al. 2003).

Other factors associated with the presence of *C. canadensis* or *C. cornuta* might also retard suckering. Both *C. canadensis* and *C. cornuta* produce prolific quantities of litter annually. The litter of *C. canadensis* can develop into a heavy thatch layer that may accumulate to depths greater than 10 cm on many sites (Lieffers et al. 1993). In the

understory of mature aspen, *C. cornuta* clumps are maintained by continuous recruitment of stems, thereby providing an annual deposition of leaf litter (Kurmis and Sucoff 1988, Mallik et al. 1997). Field studies have shown that the removal of the LFH layer can enhance aspen suckering, although these studies also resulted in some root wounding when the LFH layer was removed (Lavertu et al. 1994).

Some plant litter is known to produce allelochemicals (Rice 1984) or a combination of allelochemicals that could inhibit growth by interfering with the germination, growth or development of plants (Ben-Hammouda et al. 2002, Inderjit et al. 1995, Putnam and Tang 1986). Sparse vegetative growth has been observed under *Juglans nigra* (black walnut), owing to the allelopathic effects of drip from the canopy (Rice 1984). Foliage extract of *Rubus idaeus* var. *strigosus* (raspberry) and *Prunus serotina* (black cherry) inhibited height growth and dry weight increment of *Pinus resinosa* (red pine) seedlings (Rice 1984). The allelopathic effect of *Triticum vulgare* Punjab 81 (wheat) foliar extract reduced the growth of rice and wheat (Lodhi et al. 1987). *C. canadensis* autotoxicicty inhibited growth in low concentrations of straw extract and produced the greatest foliar damage in *C. canadensis* seedlings at intermediate concentrations of extract (Winder and Macey 2001). Litter of *C. canadensis* had negative effects on aspen seedling growth (Landhäusser and Lieffers 1998); however it is not known whether the litter affects aspen root suckering. In addition to the potential chemical effects the litter layer could also act as a physical barrier to the emergence and growth of the aspen suckers.

After a disturbance, *C. canadensis* rapidly colonizes an area by seedling establishment or from rapid spread of rhizomes within the upper 5-15cm of the soil profile (Lieffers et al. 1993, Landhäusser and Lieffers 1998, Powell and Bork 2004b). *Calamagrostis canadensis* develops thick sods of rhizomes and roots and high levels of leaf area in aspen stands that are entering the break-up stage at stand maturity. It is not clear if there are direct effects of this grass on the sucker regeneration over and above the effects of the litter. Studies have shown a reduction in the average height growth, root collar growth, stem and leaf dry weight of aspen seedlings (Lieffers et al. 1993,

Landhäusser and Lieffers 1998, Powell and Bork 2004b) as well as leaf area (Powell and Bork 2004b) of aspen seedlings grown in association with *C. canadensis*. Once suckers emerge however, there is an intense competition for light with the *C. canadensis* plants (Powell and Bork 2004a). Allelopathic effects of live plants can affect the establishment and growth of other plants in their vicinity (Rice 1984, Inderjit et al. 1995, Oueslati 2003). Horsely (1976) observed that any recruitment of *Prunus serotina* Ehrh. (black cherry) in low density cherry-maple (*Acer rubrum* L.) stands results in poor growth or mortality with dominate ground vegetation consisting of *Danthonia compressa* Aust.(wild oat grass), *Solidago rugosa* Ait. (goldenrod), *Aster umbellatus* Mill. (flat topped aster) and *Pteridium aquilinum* L. (bracken fern). In these same areas invading aspen suckers appear but have reduced vigor (Horsely 1976). Further, it is not clear if the grass is competing for nutrients during the suckering stages that might inhibit the suckering rate or growth of suckers. In studies with aspen root cuttings, the average mass of leaves, stems and roots were found to be greater in root cuttings that had high nitrogen-availability (King et al. 1999). Fraser et al. (2002) found the dry mass per sucker from root cutting to increase with fertilization. These improvements to aspen growth by fertilization could combat reductions of growth observed when aspen is growth in association with *C. canadensis* (Landhäusser and Lieffers 1998).

Objectives are to determine: 1) If suckering of aspen is affected by litter of *C. canadensis* or *C. cornuta* over and above the negative effects of this litter suppressing soil temperatures. 2) If the sod of *C. canadensis* has a direct effect of reducing suckering over and above the effects of reduced soil temperature. 3) Does fertilization reduce any competition for nutrients between the aspen suckers and *C. canadensis*.

Methods and Materials

Two greenhouse studies were conducted. The first experiment examined the effect of the litter of *C. canadensis* and *C. cornuta* on aspen suckering. The second experiment examined the rates of suckering when *C. canadensis* was grown together with aspen prior to and during the suckering process.

Aspen seedlings (plug + 1 bareroot seedlings) used for both greenhouse (litter and competition study) experiments originated from an open pollinated seed source near Peace River, Alberta (56° 14′ N, 117° 17′ W). In May 2003, a total of 110 aspen seedlings for both greenhouse studies were planted in planter boxes (16 x 56 cm x 17 cm depth) filled with a 3:1, peat to sand soil mixture. This allowed the aspen to develop a large root system. The aspen were watered whenever necessary so water was never a limiting factor. The seedlings spent one growing season outside on the University of Alberta campus, (Edmonton, Alberta) where they hardened and were stored until mid December 2003.

Litter Experiment

The litter for the experiment was collected in the fall of 2003 following leaf off. *C. cornuta* leaf litter was collected near Lac La Biche, Alberta (54° 46′ N, 111° 58′W). The *C. canadensis* litter was collected near Devon (53° 22′ N, 113° 44′ W) and near Spruce Grove, Alberta (53° 32′ N, 113° 55′ W). *Calamagrostis canadensis* samples were combined and all the litter was oven dried. A total of 66 aspen trees in the planter boxes were brought into the greenhouse in December 2003. The height and root collar diameter of each of the trees were measured and the top was then cut off at ground level. Mesh walls were constructed around the circumference of the planter boxes to contain the *C. cornuta* and *C. canadensis* litter that was evenly distributed on the surface of the boxes. Of the 66 trees, 22 were treated with 44.2 g of *C. cornuta* litter per pot (3.7 cm average hazel litter depth), 22 with 125 g of *C. canadensis* litter (8.0 cm average litter depth) and another 22 received no litter. This amount of litter is typical of what might be found accumulated on mixedwood sites dominated by each of these species. Each box was fertilized weekly with 0.7 g of 20-8-20 (nitrogen-phosphorus-potassium (N-P-K)), 0.4 g of 0-52-34 (N-P-K) and 0.1 g of micronutrients. Root systems were watered regularly so water was never a limiting factor. The greenhouse photoperiod was supplemented to 18 hours of light with 400 watt, high pressure sodium high intensity discharge (HID) fixtures and day temperature varied between 16-20 ˚C; pot position in the greenhouse was rotated weekly. Sucker emergence was monitored every day throughout the experiment.

On January 22, 2004, 30 days after the beginning of the treatments, half the pots from each litter treatment were harvested to determine if treatment response was different after different periods of growth. The total number of stump sprouts and suckers that emerged above the litter layer were recorded over the course of the experiment. At the end of the experiment suckers that had emerged through the soil but had not yet penetrated the litter were also counted. The heights (measured from the soil surface) of the stump sprouts and suckers emerging above the litter and the root collar diameter of the tallest sucker were measured. Suckers and stump sprouts were separated into leaves and shoots. Subsamples of leaves were collected at random from each sample and the leaf area was determined using a Li-Cor 3100 leaf area meter. Leaf samples were then oven dried at 68 °C and the total leaf area per planter box (cm^2) was determined. Aspen roots were washed and separated into fine and coarse roots. Roots, stems and leaves were dried at 68 °C and their weights measured. The remaining boxes continued growth for a total of 56 days when the second half of the experiment was evaluated using the same techniques as during the previous (30 day) harvest.

Competition Experiment

In early December 2003, *C. canadensis* seeds, collected from boreal forest sites near Cynthia Lake, Alberta were germinated and grown for 7 days in germination trays placed by a south-facing window. Germinates were then planted into Jiffy® 18 x 32 mm plugs and allowed to establish in a growth chamber (growth chamber conditions 18 hr, 22 °C days, 6 hr, 16 °C dark, 60 % relative humidity) for three weeks. On December 31, 2003, 44 aspen seedlings in the planter boxes were brought into the greenhouse and allowed to thaw. Half of the 44 boxes had six *C. canadensis* plugs planted per box, leaving the other 22 boxes as controls with no *C. canadensis*.

The aspen seedlings were grown with *C. canadensis* in the greenhouse with its photoperiod supplemented to 18 hours of light with sodium HID lamps at 16-20 °C. Each planters box was fertilized twice a week with 2 g/box of 20-20-20 (N-P-K), complete fertilizer. Boxes were watered whenever required (every 2 to 3 days) Late in March 2004 planter boxes were moved into a greenhouse that had cooler temperatures (8-14 °C) providing an environment which allowed the aspen to set bud and harden. In late

April 2004 grass was clipped to a 15cm height and boxes were placed in cold (ranging ±2 °C from 0 °C), dark storage for 53 days (April 29-June 21). In mid-late June 2004 boxes were removed from cold storage and placed outside and grown for the remainder of the summer. Aspen were fertilized twice a week until mid-August with 2 g/box of 20-20-20 (N-P-K), complete fertilizer and water was never limiting. All leaves were collected from the aspen in the fall of 2004 retaining sub-samples to determine the total leaf area of the trees. *Calamagrostis canadensis* was also clipped to a height of 6 cm, all biomass was oven dried at 68 °C and weighed. The aspen and *C. canadensis* plants remained outside where they hardened and spent part of the winter. The result of this pre-treatment was aspen plants with an average height of 148 cm with a large and woody root system, grown in a dense sod of *C. canadensis*.

On January 17, 2005, 32 planter boxes, 16 boxes with *C. canadensis* and 16 without were brought into the greenhouse for the study. Twelve boxes (6 with *C. canadensis* and 6 without) were removed to determine pre-treatment height, root collar diameter, coarse root mass and their carbohydrate reserves with and without *C. canadensis*. Coarse roots were extracted, ground to pass a 40 mesh screen of a Wiley mill and total sugars and starches were measured following Chow and Landhäusser (2004) (see methods Chapter II). All remaining seedlings were cut and their height and root collar diameter determined. A fertilizer treatment of 1 g of 20-20-20 N-P-K complete fertilizer per box was superimposed on half the boxes with *C. canadensis* and half of the boxes without *C. canadensis* twice a week. During the experimental period, any buds that developed on or within 1cm of the cut stump were removed to promote root suckering instead of stump sprouting. Root systems were water every other day and boxes were rotated to different positions within the greenhouse every week.

Suckering was monitored for four weeks until February 18, 2005 when boxes were harvested and the experiment ended. The total number of suckers was counted and the height and root collar diameter of the tallest sucker was recorded. Leaves were separated from shoots and a sub-sample was taken for leaf area measurements. *Calamagrostis canadensis* stems and leaves were clipped at ground level and collected. All biomass was oven dried at 68 °C and dry weights were measured. The root systems

were separated to determine the number of root suckers that had not yet emerged. Suckers that elongated above the ground were collected. The root systems of treatment control boxes and the 12 pre-treatment controls were washed and separated into coarse and fine roots. All roots were oven dried at 68°C and dry weights were measured.

Statistical Analysis

For the litter study, response variables were analyzed as a randomized 3 x 2 factorial experiment, with three litter types (*C. canadensis*, *C. cornuta* and no litter) and two times (30 and 56 days after decapitation) using a two-way analysis of variance (ANOVA). The competition experiment was a 2 x 2 factorial design with 2 levels of competition (*C. canadensis* and no competition) and two fertilization treatments (fertilizer and no fertilizer) analyzed using a two-way ANOVA. To test for pre-treatment differences between the aspen seedlings growing with and without *C. canadensis*, a simple t-test was used. All analyses used a significance level of $\alpha = 0.05$.

Results

Litter Experiment

After 30 days, a total of 8 suckers and stump sprouts had emerged through the *C. canadensis* litter compared to 16 emerging with no litter (P=0.0297, Fig. 3.1). The total number of suckers and sprouts that had emerged through the *C. cornuta* litter, however, was only reduced by 5 suckers or sprouts compared to the controls. By 56 days of growth, however, there were no differences in the number of suckers and sprouts emerging past the litter layers of *C. canadensis* or *C. cornuta* compared to the control and there was a significant interaction between time and litter effect for number of suckers not yet emerged through the litter (P=0.089). The number of suckers and sprouts that had emerged from the soil but had not broken through the *C. canadensis* litter decreased significantly from 9 at day 30 to 3 by day 56. However, when the number of suckers and sprouts above and below the litter were combined, there were no significant differences in suckering and sprouting at either day 30 or 56.

Suckers and sprouts penetrating through the litter of grass and *C. cornuta* were taller than the control treatment (Fig. 3.2), for day 30 but by day 56 height of suckers and sprouts in *C. canadensis* litter were no longer taller than the control. Root collar diameter of suckers and sprouts emerging through *C. cornuta* litter was significantly larger than that of suckers and sprouts growing either through the *C. canadensis* litter or the controls (Fig.3.3) by day 56. At day 30, total leaf area of suckers and sprouts emerging through the grass litter was reduced compared to the *C. cornuta* treatment (P=0.0001, Fig. 3.4), however, by day 56 there were no longer significant differences in total leaf area of suckers and sprouts from root systems with either *C. cornuta* or *C. canadensis* litter. However, the total leaf area of suckers and sprouts emerging through the *C. cornuta* litter were significantly greater than the total leaf area in the controls. There was no difference in the mean total dry weight of suckers and sprouts per planter box that emerged above the litter for the three litter treatments at day 30, but by day 56 the suckers and sprouts in the *C. cornuta* litter treatment had produced the highest biomass (P=0.0028, Fig. 3.5).

Competition Experiment

Prior to cutting, aspen seedlings grown with and without *C. canadensis* competition had similar root collar diameter (P=0.1859), leaf area (P=0.1564), weight of coarse roots (P=0.2520) and concentration of total non structural carbohydrates (P=0.5131).

After termination of the experiment, there were no significant treatment interactions between competition and fertilization treatments for any of the response variables. Overall, the total numbers of suckers initiated was not affected by *C. canadensis* (P=0.5401) or level of fertilization (P=0.4206, Fig. 3.6). However, aspen root systems growing together with *C. canadensis* competition had twice as many non-emerged suckers as root systems without *C. canadensis* competition (P=0.0160). This significantly reduced the number of emerged suckers from root systems with *C. canadensis*, to an average of 45 compared to 63 emerged suckers for root systems without the *C. canadensis*. The average weight of emerged suckers per root system with *C. canadensis* competition was 8.1 g, which was significantly less than the 14.4 g average weight of emerged suckers without grass (Fig. 3.7).

Aspen sucker leaf area per box was reduced by *C. canadensis* (P=0.0001). Emerged suckers grown without *C. canadensis* competition developed, on average, double the total leaf area per root system than root systems that had *C. canadensis* competition (Fig. 3.8). There was no effect of fertilization treatment on total leaf area (P=0.4001).

Discussion

Litter of *C. canadensis* had no effect on the number of suckers that were initiated but influenced the timing at which the suckers emerged through the litter into the well-lighted zone above. The physical barrier created by the litter appeared to be the main factor for this delay of emergence. In the early stages of emergence, suckers were forced to grow taller and twine their way through litter, thereby resulting in a delay of emergence. By day 56, however, nearly all root suckers produced had emerged above the litter. While in this greenhouse experiment suckers eventually were able to pass through the litter, we believe that this delay in emergence would have a large influence on the success of the suckers in field conditions. Emerging suckers in the field would not only be affected by the physical barrier of the litter but also by cool soil conditions, competitive effects and other indirect factors related to thick root sods of *C. canadensis* (Hogg and Lieffers 1990). The presence of *C. canadensis* litter has also been shown to increase mortality of aspen seedlings (Lieffers et al. 1993). Such a delay in emerging through the litter would likely further impede establishment of the aspen suckers.

The *C. cornuta* litter had little negative effect on the rate of emergence of suckers and actually appeared to stimulate the growth of suckers relative to the controls. *C. cornuta* litter could be contributing increased concentration of available nutrients under its canopy, especially Ca and Mn due to the rapid decomposition of the leaves (Tappeiner and Alm 1972). Similarly, decaying ivy leaves had stimulatory effects on root and shoot growth of both radish and downy brome growth (Putnam and Tang 1986). It is not clear if the growth stimulation of the aspen suckers was caused by nutrients or beneficial allelochemicals released from the *C. cornuta* litter (Rice 1984, Putnam and Tang 1986). These positive effects might be negated in the field due to competition of *C. cornuta* for

resources and growing space. For example, the extensive and complex intertwining *C. cornuta* rhizomes and roots would likely impede sucker emergence similarly to the *C. canadensis* sods. Further, the below ground biomass of *C. cornuta* is nearly equal to the above ground biomass providing a high potential for sprouting of *C. cornuta* (Mallik et al. 1997). This intense sprouting, which Mallik et al. (1997) found to be greater than aspen suckering, could result in intense, direct, competition for light with the emerging aspen suckers (Best et al. 2003).

In the absence of accumulated *C. canadensis* sods had no apparent effect on the total number of suckers initiated on the root system but did result in a significant decrease in the number of suckers that emerged from the soil. Also, the suckers that emerged were on average smaller and had less leaf area than suckers from root systems that had no *C. canadensis* competition. This is similar to findings of Powell and Bork (2004a) who report that aspen seedling growth and mass were reduced in the presence of *C. canadensis*. As there was no difference in the size and carbohydrate reserves between the root systems of aspen with or without *C. canadensis* prior to suckering, and all plants were provided with sufficient light, water and nutrients prior to decapitation, competition effects prior to the experiment can be eliminated as a reason for the difference in the suckering performance. More likely, the thick mat of *C. canadensis* roots and rhizomes acted as a physical barrier to emerging suckers. This would explain why few suckers emerged above the soil. It is also possible that the roots and rhizomes of *C. canadensis* could have had an allelopathic influence on the development of the aspen suckers as allelopathy is closely associated with competition between plants (Inderjit et al. 1995). Thus, the delay in emergence related to a dense root system of the grass would add further to the list of impediments to the emergence and growth of the aspen root suckers (cold soils, the impediment of grass litter and direct competition for light) that characterize dense beds of *C. canadensis* (Hogg and Lieffers 1990, Lieffers et al. 1993, Frey et al. 2003). With the presence of competition that reduces sucker emergence and growth, fewer suckers will attain the height necessary to outcompete shrubs and grass and become well established trees (De Blois et al. 2004).

Fertilization did not provide any advantages to the number of suckers initiated or the growth of suckers. Czapowskyj and Safford (1997) also observed that fertilization with urea ($(NH_2)_2CO$) provided no benefit to mature aspen in regards to height and volume growth. There was also no benefit to aspen growth when fertilized with ammonium nitrate (NH_4NO_3) (van den Driessche et al. 2003, van den Driessche et al. 2005). This is in contrast to findings of King et al. (1999) who observed larger aspen seedlings from root cuttings as a result of fertilization regardless of soil temperature and Fraser et al. (2002) who found suckers from root cuttings had increased sucker dry mass following fertilization with ammonium nitrate. The choice of fertilizer may have resulted in the lack of improved growth in suckers receiving the fertilizer treatment. Only about 40% of the nitrogen in the fertilizer was nitrate, a form that aspen has shown preference for (Min et al. 1998, Min et al. 2000, Frey et al. 2003, Choi et al. 2005). It appears that high levels of ammonium did not translate into any growth advantage (Kronzucker et al. 2003).

Conclusion

Results from these studies clearly indicate that *C. canadensis* sods and litter provided a physical barrier to the emergence of aspen suckers that resulted in a delay of emergence. In the field, cold soils and light competition would further impede aspen sucker establishment. *C. cornuta* litter appears to promote rather than impede the growth of aspen suckers, which suggests that negative effects of *C. cornuta* on sucker development are likely from above and below ground competition. In these experiments fertilization did not result in any growth advantage.

Figure 3.1. Total number of emerged aspen suckers found above and below the *C. canadensis* and *C. cornuta* litter layers or in the controls after 30 and 56 days of growth (n=11). The number of suckers found above and below the litter were analyzed separately. Treatment means with the same letter are not significantly different.

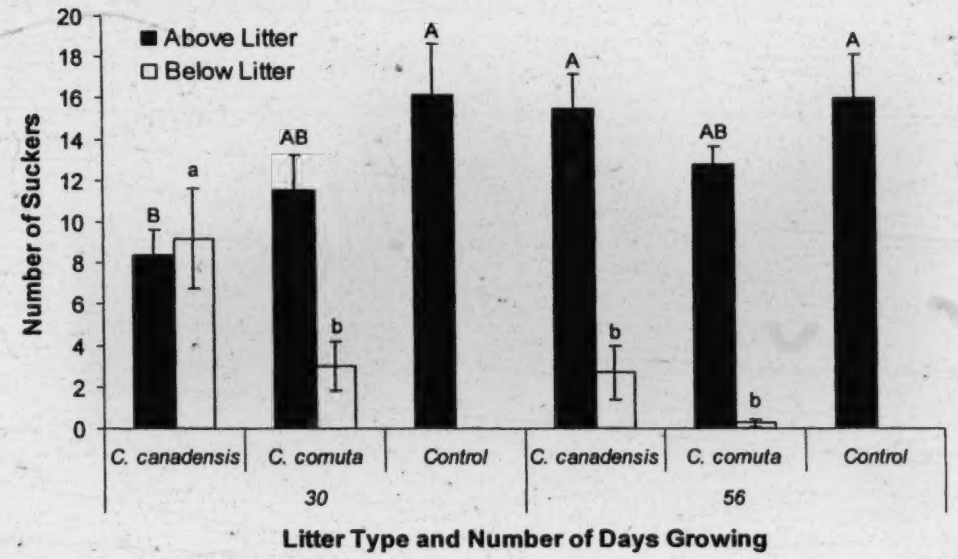


Figure 3.2. Average height of aspen suckers that had emerged above the litter layer of *C. canadensis* or *C. cornuta* or above the soil of the control after 30 and 56 days of growth (n=11). Means with the same letter are not significantly different.

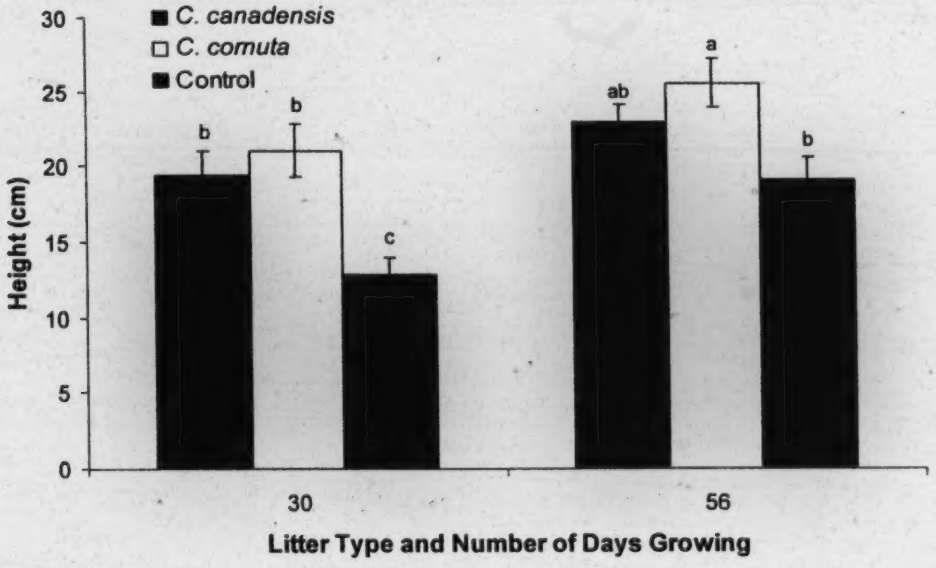


Figure 3.3. Average root collar diameter of aspen suckers that had emerged above the *C. canadensis* or *C. cornuta* litter or above the soil for the control, after 30 or 56 days of growth (n=11). Means with the same letter are not significantly different.

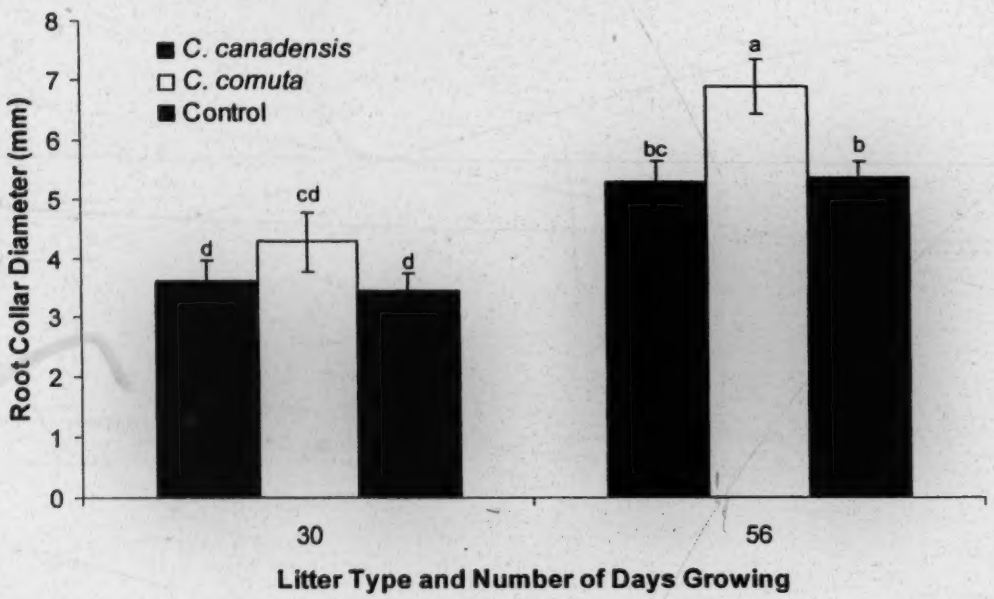


Figure 3.4. Total leaf area of aspen suckers that had emerged above the *C. canadensis* or *C. cornuta* litter or above the soil for the control, after 30 or 56 days of growth (n=11). Means with the same letter are not significantly different.

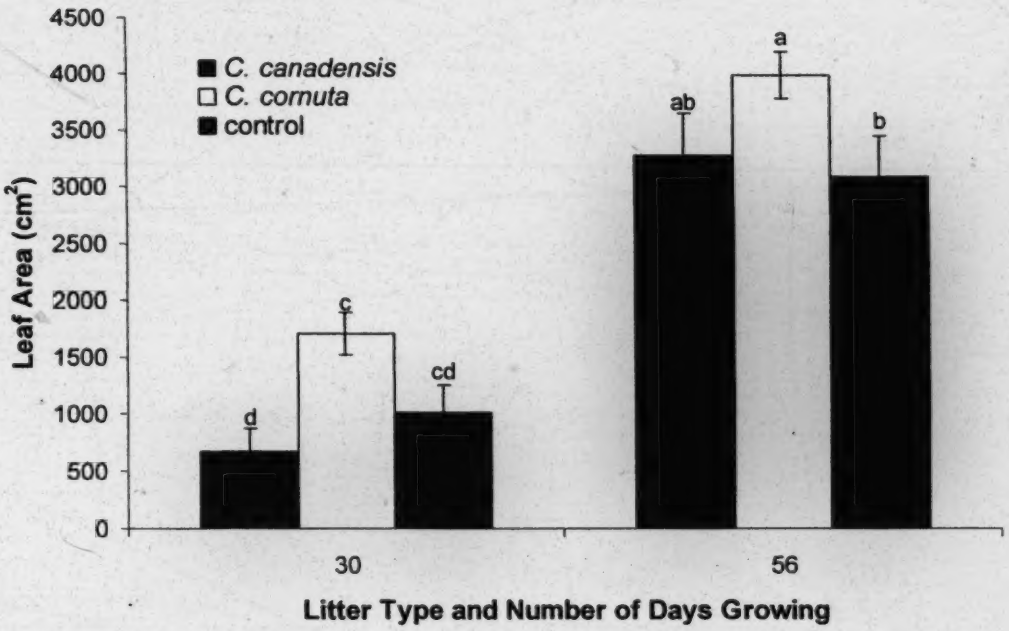


Figure 3.5. Total weight of aspen suckers that had emerged above the *C. canadensis* or *C. cornuta* litter or above the soil for the control, after 30 or 56 days of growth (n=11). Means with the same letter are not significantly different.

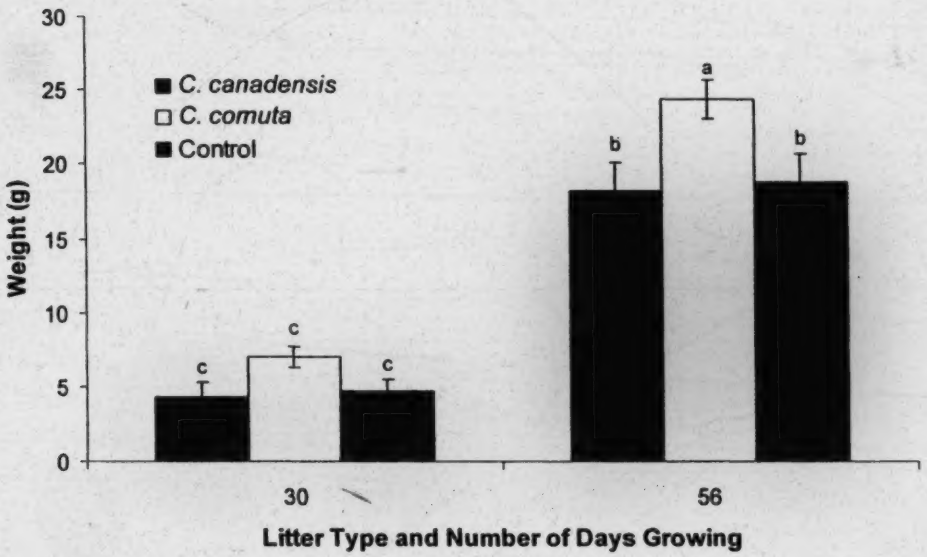


Figure 3.6. The average number of aspen suckers that emerged above the soil and suckers still below the soil (non-emerged, elongated root buds) from root systems with or without *C. canadensis* sods (n=16). The number of emerged and non-emerged suckers were analyzed separately. Treatment means with the same letter are not significantly different.

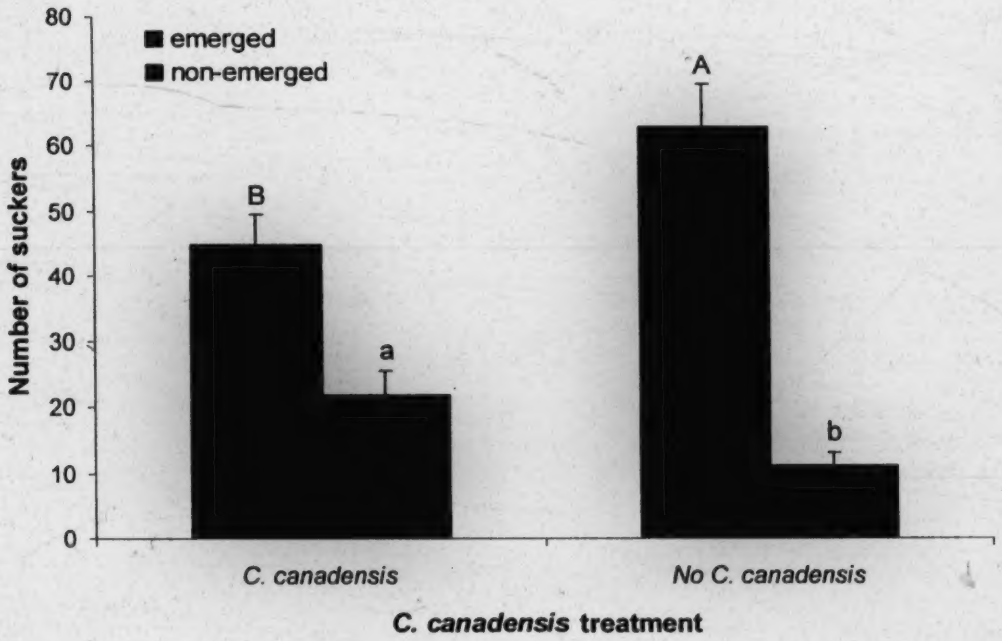


Figure 3.7. Average weight of aspen suckers emerged above the soil, from root systems with or without *C. canadensis* sods (n=16). Means with the same letter are not significantly different.

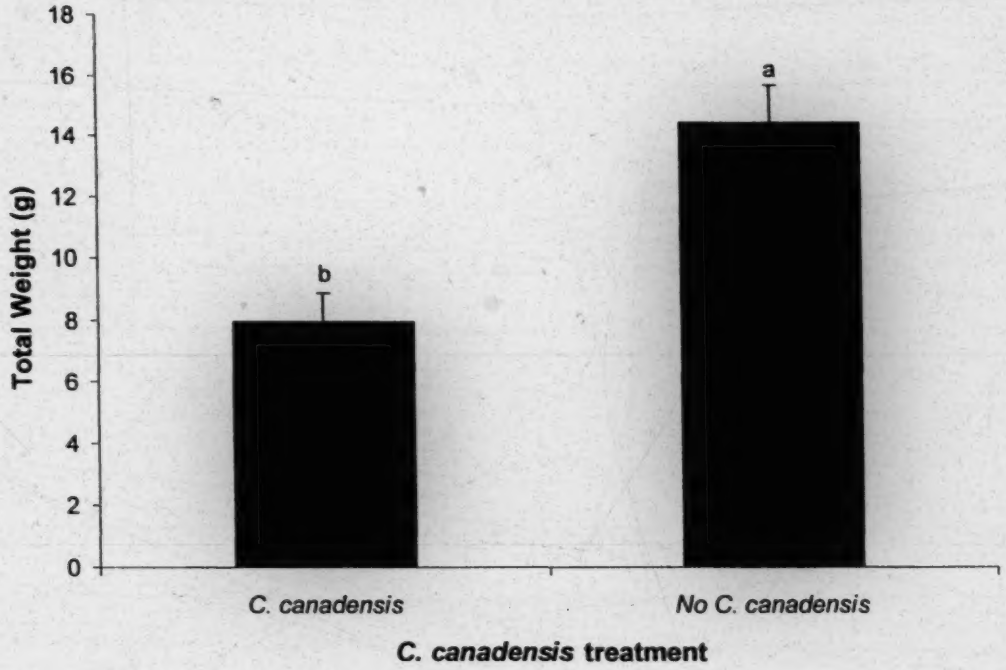
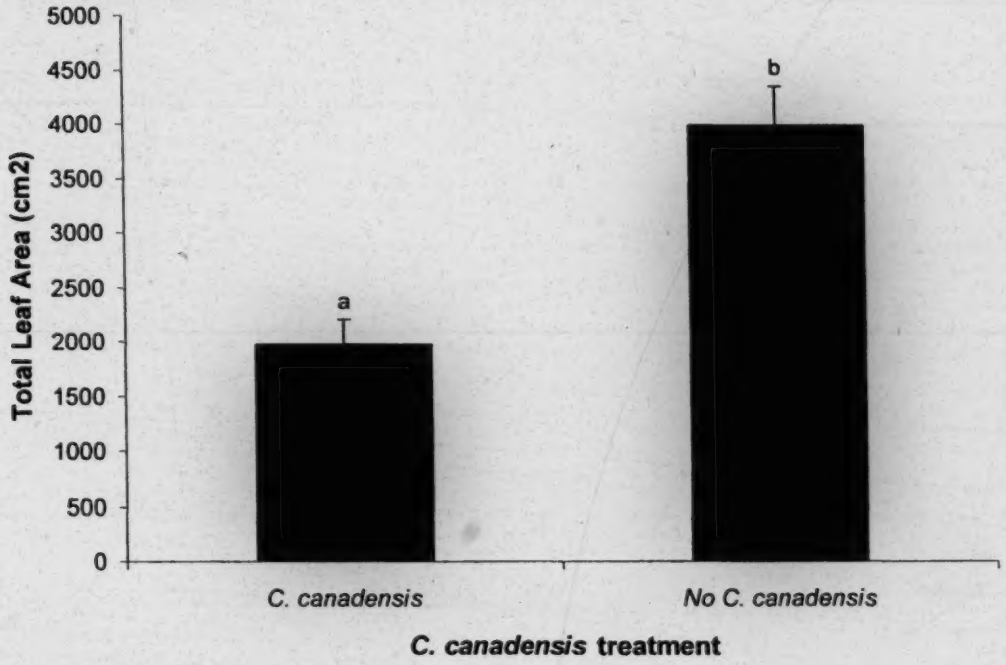


Figure 3.8. Total leaf area of aspen suckers per planter box emerged above the soil, from root systems with or without *C. canadensis* sods (n=16). Means with the same letter are not significantly different.



References

Bates, P.C., Blinn, C.R., and Alm, A.A. 1993. Harvesting impacts on quaking aspen regeneration in northern Minnesota. Can. J. For. Res. 23: 2403-2412.

Ben-Hammouda, M., Ghorbal, H., Kremer, R.J., and Oueslatt, O. 2002. Autotoxicity of Barley. J. Plant Nut. 25(6): 1155-1161.

Best, J.N., Bork, E.W., and Cool, N.L. 2003. Initial beaked hazel growth responses following protection from ungulate browsing. J. Range. Manage. 56: 455-460.

de Blois, S., Brisson, J., and Bouchard, A. 2004. Herbaceous covers to control tree invasion in rights-of-way: Ecological concepts and applications. Environ. Manag. 33(5): 606-619.

Choi, W.-J., Chang, S.X., and Hao, X. 2005. Soil retention, tree uptake, and tree resorption of $^{15}NH_4NO_3$ and $NH_4{}^{15}NO_3$ applied to trembling and hybrid aspens at planting. Can. J. For. Res. 35: 823-831.

Chow, P.S., and Landhäusser, S.M. 2004. A method for routine measurements of total sugar and starch content in woody plant tissues. Tree Phys. 24: 1129-1136.

Crouch, G.L. 1986. Aspen regeneration in 6- to 10-year-old clearcuts in southwestern Colorado. USDA For. Serv. Res. Note RM-467.

Czaposkyj, M.M., and Safford, L.O. 1997. Growth response to fertilizer in a young aspen-birch stand. USDA For. Serv. Res. Note NE-274.

Day, M.W. 1944. The root system of aspen. Am. Midl. Nat. 32:502-509.

Doucet, R.1989. Regeneration silviculture of aspen. For. Chron. 65: 23-27.

Farmer, R.E. 1962. Aspen root sucker formation and apical dominance. For. Sci. 8: 403-410.

Fraser, E.C., Lieffers, V.J., Landhäusser, S.M., and Frey, B.R. 2002. Soil nutrition and temperature as drivers of root suckering in trembling aspen. Can. J. For. Res. 32: 1685-1691.

Frey, B.R., Lieffers, V.J., Landhäusser, S.M., Comeau, P.G., and Greenway, K.J. 2003. An analysis of sucker regeneration of trembling aspen. Can. J. For. Res. 33: 1169-1179.

Hogg, E.H., and Lieffers, V.J. 1991. The impact of *Calamagrostis canadensis* on soil thermal regimes after logging in northern Alberta. Can. J. For. Res. 21: 387-394.

Horsely, S.B. 1976. Allelopathic inhibition of black cherry by fern, grass goldenrod, and aster. Can. J. For. Res. 7: 205-216.

Inderjit, Dakahini, K.M.M., and Einhellig, F.A. 1995. ACS Symposium Series 582 Allelopathy: organisms, processes, and applications. American Chemical Society, Washington D.C.

Jones, J.R., and Trujillo, D.P. 1975. Development of some young aspen stands in Arizona. USDA For. Serv. Res. Pap. RM-151.

King, J.S., Pregitzer, K.S., and Zak, D.R. 1999. Clonal variation in above- and below-ground growth responses of *Populus tremuloides* Michaux: Influence of soil warming and nutrient availability. Plant Soil 217: 119-130.

Kronzucker, H.J., Siddiqi, M.Y., Glass, A.D.M., and Britto, D.T. 2003. Root ammonium transport efficiency as a determinant in forest colonization patterns: an hypothesis. Physiol. Plant. 117: 164-170.

Kurmis, V., and Sucoff, E. 1988. Population density and height distribution of *Corylus cornuta* in undisturbed forests of Minnesota: 1965 – 1984. Can. J. Bot. 67: 2409-2413.

Landhäusser, S.M., and Lieffers, V.J. 1998. Growth of *Populus tremuloides* in association with *Calamagrostis candensis*. Can. J. For. Res. 28: 396-401.

Lavertu, D., Mauffette, Y., and Bergeron, Y. 1994. Effects of stand age and litter removal on the regeneration of *Populus tremuloides*. J. Veg. Sci. 5: 561-568.

Lieffers, V.J., Macdonald, S.E., and Hogg, E.H. 1993. Ecology of and control strategies for *Calamagrostis canadensis* in boreal forest sites. Can. J. For. Res. 23: 2070-2077.

Lodhi, M.A.K., Bilal, R., and Malik, K.A. 1987. Allelopathy in agroecosystems: Wheat phytotoxicity and its possible roles in crop rotation. J. Chem. Ecol. 13: 1881-1891.

Mallik, A.U., Bell, F.W., and Gong, Y. 1997. Regeneration behavior of competing plants after clear cutting: implications for vegetation management. For. Ecol. Manage. 95: 1-10.

Min, X., Siddiqi, M.Y., Guy, R.D., Glass, A.D.M., and Kronzucker, H.J. 1998. Induction of nitrate uptake and nitrate reductase activity in trembling aspen and lodgepole pine. Plant Cell Environ. 21(10): 1039-1046.

Min, X., Siddiqi, M.Y., Guy, R.D., Glass, A.D.M., and Kronzucker, H.J. 2000. A comparative kinetic analysis of nitrate and ammonium influx in two early-successional tree species of temperate and boreal forest ecosystems. Plant Cell Environ. 23: 321-328.

Oueslati, O. 2003. Allelopathy in two durum wheat (*Triticum durum* L.) varities. Agric. Ecosystems and Environ. 96: 161-163.

Powell, G.W., and Bork, E.W. 2004a. Above- and below-ground effects from alfalfa and marsh reedgrass on aspen seedlings. For. Ecol. Mange. 199; 411-422.

Powell, G.W., and Bork, E.W. 2004b. Competition and facilitation in mixtures of aspen seedlings, alfalfa, and marsh reedgrass. Can. J. For. Res. 34: 1858-1869.

Putnam, A.R., and Tang, C.-S. 1986. The science of allelopathy. John Wiley & Sons, Inc., New York.

Rice, E.L. 1984. Allelopathy 2nd ed. Academic Press, Inc., Orlando, Fla.

Stoeckeler, J.H., and Macon, J.W. 1956. Regeneration of aspen cutover areas in northern Wisconsin. J. For. 54: 13-16.

Steneker, G.A. 1976. Guide to the silvicultural management of trembling aspen in the prairie provinces. Can. For. Serv. North. For. Cent. Inf. Rep. NOR-X-164.

Tappeiner, J.C., and Alm, A.A. 1972. Effect of hazel on the nutrient composition of annual litter and forest floor in jack and red pine stands. Minnesota For. Res. Note. 235.

Van den Driessche, R., Rude, W., and Martens, L. 2003. Effect of fertilization and irrigation on growth of aspen (*Populus tremuloides* Michx.) seedlings over three seasons. For. Ecol. Manage. 186: 381-389.

Van den Driessche, R. Niemi, F., and Charleson, L. 2005. Forth year response of aspen seedlings to lime, nitrogen and phosphorus applied at planting and 1 year after planting. For. Ecol. Manage. Article in Press.

Winder, R.S., and Macey, D.E. 2001. The influence of edaphic and competitive factors on productivity of marsh reed grass (Calamagrostis Canadensis) in a cooperative pathosystem. Can. J. Bot. 79: 805-814.

Zehngraff, P.J. 1946. Season of cutting affects aspen sprouting. USDA For. Serv. Lake States For. Exp. Sta. Tech. Note 250.

CHAPTER IV

Research Summary, Implications and Future Research

Trembling aspen (*Populus tremuloides* Michx.) is a clonal tree species that primarily regenerates vegetatively via root suckers and stump sprouts after a disturbance removes the above ground portions of the clone. Chapter II describes an experiment that determined if the density of aspen regeneration in juvenile mixedwood stands of aspen and white spruce could be controlled by thinning regimes at specific times of year thereby promoting the white spruce. Regeneration after mature stands are harvested is known to be prolific and is commonly controlled by manually cutting in regenerating mixedwood stands when the white spruce is the desired species. Season of harvest also is known to affect regenerating densities. A field study examined if the density of residual trees or specific season of thinning of juvenile stands could reduce the amount of aspen resprouting and resuckering. In contrast, Chapter III determined the potential negative effects of the presence of *Calamagrostis canadensis* Michx or *Corylus cornuta* Marsh (beaked hazelnut) on the sucker regeneration of aspen. Reduced growth and vigor of aspen regeneration can be associated with a thick litter layer and competition with other vegetation. Greenhouse studies were established to determine if there are effects of *C. canadensis* and *C. cornuta* litter and *C. canadensis* competition on suckering of the aspen root systems.

Residual Density and Time of Thinning

Maintaining a residual density of aspen of 1,500 stems per hectare (sph) significantly reduced the re-suckering and re-sprouting of aspen compared to complete removal. However, after one growing season the regeneration densities in the 1,500 sph residual density treatment (up to 56,000 sph) were still too great to merit operational implementation of this thinning technique to lower the density of aspen in mixedwood stands. However, with 1,500 residual stems per hectare, regeneration may be suppressed

following canopy closure by the residual trees. There could also be a redistribution of growth into the dominant residual stems over the regeneration further suppressing the stump sprouts and suckers (Mowrer 1988). The timing of thinning, however, had no significant effect on the density of the re-sprouting and re-suckering aspen. Root suckers are the primary source of regeneration after harvesting mature aspen stands. In contrast, cutting 10 year old stems resulted in stump sprouting as the dominant means of regeneration.

At the beginning of the first growing season after thinning, total nonstructural carbohydrate (TNC) concentrations in roots with sprouts or suckers dropped significantly compared to TNC concentrations in the roots of the residual trees and control trees. However, by the end of the first growing season, the TNC reserves of roots that had sprouted and suckered had recovered to levels similar to roots that were adjacent to and connected to residual trees or the control trees. Roots from regeneration in the 1,500 sph thinning treatment had significantly lower TNC reserves than roots of the residuals and controls, presumably because there were fewer residual and regenerating stems, with less leaf area to contribute to rebuilding carbohydrate reserves into the roots. In the examination of the roots with regenerating sprouts, those from winter cutting treatments had greater TNC concentration than those cut in spring and summer.

This study suggests that the timing of removal makes little difference in how many stems regenerate, but there was slightly less vigorous regeneration when the cutting was done in the spring season. Maintaining some residual trees (ramets) at the time of harvesting of mature stands is known to reduce the density of regenerating stems (Stoeckeler and Macon 1956, Steneker 1976, Schier and Smith 1979, Lavertu et al. 1994, Huffman et al. 1999) and this was also the case in this study.

There have been contradictory findings regarding which time or phenological stage mature aspen stands should be harvested to either increase or reduce aspen regeneration. Many studies deem summer harvesting to produce the least amount of suckers compared to winter harvesting (Zengraff 1946, Bates et al. 1993, Bell et al. 1999) while others support the opposite view (Bella 1986). This study was better replicated than these studies, had operational sized plots and was not confounded by differences in

logging damage between winter and summer. This study showed only minimal differences in re-suckering and re-sprouting between different phenological stages or seasons of thinning for the 10-year-old aspen. However, height growth of sprouts and suckers was significantly lower in plots cut in the spring verses winter. This reduced height alone however, does not advocate spring as a preferred thinning season due to the high regenerating density (average of 72,000 sph). In a review of aspen thinning studies Mowrer (1988) reported that sucker height may not be an indicator of future growth potential of a stand as height growth is more dependent on site quality.

There are a multitude of factors, both positive and negative, on aspen suckering that are associated with the effect of season of cutting. The higher soil temperatures and the removal of competitive vegetation associated with summer harvesting can be beneficial to aspen suckering (Bates et al. 1989). Conversely, risk of damage by early fall frosts to the newly emerged suckers and lower root carbohydrate reserves following leaf flush in spring and early summer may reduce sucker emergence and growth (Bates et al. 1989). A higher intensity of light competition could be associated with summer thinning as sucker emerge after full leaf out of competing vegetation (Bates et al. 1989, Frey et al. 2003). The positive aspects of winter harvest include providing suckers with a full growing season in their first year. Winter harvest is expected to result in higher carbohydrate reserves in the roots at time of sprouting; in contrast it has been widely thought that lowest reserves are after leaf flush. My study showed root TNC in the 10-year-old trees to be highest in the fall then decline through the winter and reach their lowest concentrations after leaf flush in the spring. Although there was no difference in the densities of aspen regeneration between seasons of thinning, the lower TNC concentration found in roots at the time of spring thinning may be responsible for the shorter stump sprouts and suckers in the spring treatments.

Litter and Competition

In some instances aspen stands that have been harvested fail to regenerate into fully stocked stands. One of the factors influencing sucker success could be the litter layer. A litter layer can physically impede suckers thereby delaying emergence and may

provide a shaded environment with low light intensities filtering down through the litter that can reduce growth of suckers (Frey et al. 2003). A thick LFH layer may act as a thermal insulator resulting in a delay of soil warming in the spring and cool soils are known to reduce the growth of aspen seedlings (Landhäusser and Lieffers 1998). A delay in sucker emergence and reduced sucker growth may hinder aspen sucker establishment by shortening the length of the growing season for the aspen and allowing competing vegetation to develop leaf area thereby capturing the light resource (Frey et al. 2003). Removal of litter of *C. canadensis* should thus have a positive effect upon the sucker regeneration of aspen. The physical barrier to emerging suckers produced by the litter would be removed and a greater intensity of light could potentially reach the soil surface. Removing the litter layer and any insulating effects produced by the litter could provide warmer soils that would be advantageous to aspen sucker growth (Landhausser and Lieffers 1998, Frey et al. 2003). Studies have shown improved growth with removal of the LFH layer (Alban et al. 1994, Lavertu et al. 1994, Landhäusser and Lieffers 1998, Stone and Elioff 1998).

My study is the first to directly test the effect of litter on sucker initiation and early growth, independent of the effects of cold soil associated with litter. The direct effects of litter appeared mostly to be related to a physical impediment delaying sucker emergence. However, numbers of suckers emerging through the litter and their growth was able to recover to the level of the controls when given sufficient time to grow (56 days). Likely the recovery was aided in part by the exclusion of other effects such as reduced soil temperature and aboveground shading. In a field situation this same recovery may not occur due to the additive effects of the cold soil temperatures and competition. Surprisingly, *C. cornuta* litter did not have negative effects on suckering. In fact, aspen suckers grown in the presence of *C. cornuta* litter were somewhat larger than the controls but had overall fewer suckers although not significantly. The stimulation of sucker growth may be linked to the higher amounts of root carbohydrates reserves distributed over fewer stems. However, stimulatory allelochemicals from the *C. cornuta* litter could also have contributed to the growth of these suckers. It can be speculated that the competitive effects of *C. cornuta* observed in the field is more likely

due to this shrubs direct competition between aspen for the resources of light, water and nutrient and growing space.

I also tested the direct competition of *C. canadensis* grass with the aspen, by growing the aspen in large pots with or without the grass. The aspen was then decapitated and the suckering response was recorded in these pots with and without a sod of *C. canadensis*. The number of suckers initiated on the root systems of the aspen were similar between pots with and without *C. canadensis* plants. *Calamagrostis canadensis* sods, however, did significantly inhibit the emergence of suckers above the soil surface. Potentially the physical barrier produced by dense *C. canadensis* sods comprised of fine roots and rhizomes was responsible for the reduced emergence. However it remains unclear what role if any allelopathy may have played in the reduced number and growth of aspen suckers. Similarly, with aspen seedlings, growth was hampered when grown in association with *C. canadensis* (Lieffers et al. 1993, Landhäusser and Lieffers 1998, Powell and Bork 2004a, Powell and Bork 2004b). Interestingly, fertilization did not improve the early growth of aspen suckers, suggesting that the competition for nutrients may have played only a minor role in the competitive effects on early growth of suckers. In a field setting, competition for light and water and reduced soil temperatures may be the dominant inhibitory effects of *C. canadensis* towards aspen suckers, but these were not the focus of my study.

Management Implication

The results from chapter II show a reduction in the density of regenerating stems with a residual juvenile aspen canopy. In practice however, the benefits of leaving some juvenile residual stems provided too little control to implement a one time manual cut. It is likely that multiple cuttings will still be required to remove enough of the aspen for spruce seedlings to meet free to grow standards. Although time of thinning had no significant effect on the density of resprouting and resuckering, manual thinning in the spring reduced height growth of regeneration at that time compared to the other seasons. Litter and competition had no effect on sucker bud initiation, however, sucker emergence through both litter layers and the sods of *C. canadensis* was delayed. *Calamagrostis*

canadensis sods reduced aspen sucker numbers and their growth. Mechanical site preparation that removes *C. canadensis* and *C. cornuta* litters and *C. canadensis* competition may be implemented more often as a management option to improve the rate of emergence and the growth and vigor of aspen regeneration.

Future Research

There are a number of areas that need future research:

1) There is still not a clear consensus regarding if harvesting or thinning at a specific phenological stage or season can reduce or promote aspen regeneration. My study suggests that there were relatively weak differences in growth between the different seasons of thinning of the juvenile aspen in the field study (Chapter II). In operational harvest, however, there are confounding factors that are created by the way that season of cut affects soil compaction, removal/destruction of competing vegetation and disturbance of the LFH layer. These factors therefore need to be assessed in terms of their contribution to the success or failure of aspen regeneration at different seasons of cut.
2) *Corylus cornuta* litter did not have a negative effect on aspen suckering (Chapter III). However, if *C. cornuta* exists in the understory of an aspen stand prior to cutting it can make up a large portion of the canopy that re-sprouts after disturbance. This was observed in the field study (Chapter II). Although the litter did not have negative implications in the second greenhouse study there are other competitive effects of this shrub that should be considered in greater detail. *Corylus cornuta* typically grow in large clumps, with dense beds of 1-2m tall stems that will compete with aspen suckers for light and space. Its extensive below ground biomass of intertwining roots and rhizomes is nearly equal to the above ground biomass and likely impedes aspen sucker emergence through competition for moisture, nutrients and growing space.
3) Allelopathic effects of *C. canadensis* on aspen suckering and growth has been suggested by many authors to be important in affecting growth of associated species. It is unclear from findings of the greenhouse studies if *C. canadensis*

competition or its litter demonstrates allelopathy. It is difficult to distinguish between allelopathy and competition because they often occur simultaneously. To achieve a clearer understanding, the allelopathy of *C. canadensis* should be examined without the confounding effects of competition. This might be done using leachates from the grass litter or roots exudates.

4) Fertilization may improve aspen regeneration. While there are several studies that have shown improved aspen growth with fertilization there are also a number of studies, including this study that did not see any beneficial effects. It was speculated in Chapter III that the low amount of nitrate compared to other forms or nitrogen in the fertilizer may have been responsible for the lack of improved growth. I suggest directly testing ammonium (NH_4^+) effects against nitrate (NO_3^-) effects on aspen sucker growth or varying levels of these forms of nitrogen.

References

Alban, D.H., Host, G.E., Elioff, J.D., and Shadis, D. 1994. Soil and vegetation resonse to soil compaction and forest floor removal after aspen harvesting. USDA For. Serv. Res. Pap. NC-315.

Bates, P.C., Blinn, C.R., and Alm, A.A. 1993. Harvesting impacts on quaking aspen regeneration in northern Minnesota. Can. J. For. Res. 23: 2403-2412.

Bates, P.C., Blinn, C.R., Alm, A.A., and Perala, D.A. 1989. Aspen stand development following harvest in the Lake States Region. North. J. Appl. For. 6: 178-183.

Bell, F.W., Lautenschlager, R.A., Wagner, R.G., Pitt, D.G., Hawkins, J.W., and Ride, K.R. 1997. Motor-manual, mechanical, and herbicide release affect early successional vegetation in northwestern Ontario. For. Chron. 73(1): 61-68.

Bell, F.W., Pitt, D.G., Morneault, A.E., and Pickering, S.M. 1999. Response of immature trembling aspen to season and height of cut. North. J. Appl. For. 16(2): 108-114.

Bella, I.E. 1986. Logging practices and subsequent development of aspen stands in east-central Saskatchewan. For. Chron. 62: 81-83.

Huffman, R.D., Fajvan. M.A., and Wood, P.B. 1999. Effects of residual overstory on aspen development in Minnesota. Can. J. For. Res. 29: 284-289.

Landhäusser, S.M., and Lieffers, V.J. 1998. Growth of *Populus tremuloides* in association with *Calamagrostis candensis*. Can. J. For. Res. 28: 396-401.

Lavertu, D., Mauffette, Y., and Bergeron, Y. 1994. Effects of stand age and litter removal on the regeneration of *Populus tremuloides*. J. Veg. Sci. 5: 561-568.

Lieffers, V.J., Macdonald, S.E., and Hogg, E.H. 1993. Ecology of and control strategies for *Calamagrostis canadensis* in boreal forest sites. Can. J. For. Res. 23: 2070-2077.

Mowrer, H.T. 1988. Is managing aspen density worthwhile? In: Proceedings – Future Forests of the Mountain West: A stand culture symposium. W.C. Schmidt (compiler). USDA For. Serv. Gen. Tech. Rep. INT-243. pp. 201-209.

Powell, G.W., and Bork, E.W. 2004a. Competition and facilitation in mixtures of aspen seedlings, alfalfa, and marsh reedgrass. Can. J. For. Res. 34: 1858-1869.

Powell, G.W., and Bork, E.W. 2004b. Above- and below-ground effects from alfalfa and marsh reedgrass on aspen seedlings. For. Ecol. Mange. 199: 411-422.

Schier, G.A., and Smith, A.D. 1979. Sucker regeneration in Utah aspen clone after clearcutting, partial cutting, scarification, and girdling. USDA For. Serv. Res. Note INT-253.

Steneker, G.A. 1976. Guide to the silvicultural management of trembling aspen in the prairie provinces. Can. For. Serv. North. For. Cent. Inf. Rep. NOR-X-164.

Stoeckeler, J.H., and Macon, J.W. 1956. Regeneration of aspen cutover areas in northern Wisconsin. J. For. 54: 13-16.

Stone, D.M., and Elioff, J.D. 1998. Soil properties and aspen development five years after compaction and forest floor removal. Can. J. Soil Sci. 78: 51-58.

Zehngraff, P.J. 1946. Season of cutting affects aspen sprouting. USDA For. Serv. Lake States For. Exp. Sta. Tech. Note 250.

APPENDIX A. Means of aspen response variables.

Table A1. Density of total amount of regeneration and clusters with separated into stump sprouts and suckers for each treatment (n=27). Treatment means with the same letter in columns and within treatments are not significantly different.

Residual treatment density	total stems/Ha	stumps sprouts	suckers	total number of clusters	sprouted stumps (clusters)	suckers (clusters)
0	91173[a]	82049[a]	9123[a]	26296[a]	20420[a]	5877[a]
500	70395[b]	63951[b]	6444[ab]	20173[b]	16198[b]	3975[b]
1500	55741[c]	51272[b]	4469[b]	18407[b]	15593[b]	2815[b]
Time of thinning						
summer	69148[a]	61877[a]	7272[a]	20827[a]	16074[a]	4753[a]
winter	76346[a]	71160[a]	5185[a]	21889[a]	18667[a]	3222[a]
spring	71815[a]	64235[a]	7580[a]	22160[a]	17469[a]	4691[a]

Table A2. Densities of stump sprouts, suckers and total regenerating stems (stump sprouts and suckers) in relation to time of thinning and number of residual stems retained (n=9).

Time of thinning	Residual treatment density	Total regeneration	Sprouted stumps	Suckers	% of stump sprouts
summer	0	87926 ± 15020	77481 ± 15519	10444 ± 2988	88
summer	500	70556 ± 17797	63111 ± 17120	7444 ± 3837	89
summer	1500	48963 ± 10576	45037 ± 11676	3926 ± 3550	92
winter	0	104889 ± 10115	96741 ± 10137	8148 ± 2625	92
winter	500	64481 ± 10563	61037 ± 10724	3444 ± 962	95
winter	1500	59667 ± 15229	55704 ± 15420	3963 ± 2928	93
spring	0	80704 ± 11611	71926 ± 10754	8778 ± 1508	89
spring	500	76148 ± 9101	67704 ± 9045	8444 ± 8444	89
spring	1500	58593 ± 13101	53704 ± 13122	5519 ± 1884	92

Table A3. Total leaf area and height of regeneration including standard errors for each combination of time of thinning and density of residual stems (n=9).

Time of thinning	Residual treatment density	Leaf area index (m^2/m^2)	Height (cm)
summer	0	0.603 ± 0.247	82.067 ± 6.743
summer	500	0.299 ± 0.185	68.889 ± 7.602
summer	1500	0.215 ± 0.169	70.888 ± 7.368
winter	0	0.742 ± 0.324	85.688 ± 4.640
winter	500	0.358 ± 0.254	73.850 ± 8.386
winter	1500	0.393 ± 0.372	80.361 ± 9.532
spring	0	0.626 ± 0.264	80.790 ± 2.709
spring	500	0.369 ± 0.257	57.461 ± 6.845
spring	1500	0.228 ± 0.231	53.724 ± 5.101

APPENDIX B. Means of response variables for shrubs and grass.

Table B1. Densities of re-sprouting after the first growing season after treatment for alder (n=3), hazel (n=3) and willow (n=10). Grass (*Calamagrostis canadensis*) percentage cover was also estimated (n=10). (± standard errors).

Time of thinning	Residual treatment density	Alder sprout density (sph)	Hazel sprout density (sph)	Willow sprout density (sph)	% grass cover
summer	0	14 ± 9	10 ± 8	34 ± 6	14 ± 5
summer	500	3 ± 3	18 ± 10	31 ± 6	7 ± 2
summer	1500	8 ± 8	26 ± 15	32 ± 8	9 ± 2
winter	0	7 ± 6	33 ± 23	22 ± 2	3 ± 1
winter	500	12 ± 11	2 ± 3	16 ± 5	13 ± 4
winter	1500	18 ± 10	21 ± 20	18 ± 2	11 ± 5
spring	0	14 ± 5	13 ± 12	39 ± 9	8 ± 3
spring	500	20 ± 5	1 ± 1	8 ± 1	8 ± 5
spring	1500	10 ± 7	18 ± 12	15 ± 2	7 ± 2
control		10 ± 6	12 ± 9	4 ± 1	11 ± 3

Table B2. Heights of re-sprouting alder (n=3), hazel (n=3) and willow (n=10) and estimated % grass (*Calamagrostis canadensis*)cover including standard errors. (± standard errors).

Time of thinning	Residual treatment density	Alder sprout height (cm)	Hazel sprout height (cm)	Willow sprout height (cm)	% grass cover
summer	0	61.55 ± 7.67	57.83 ± 13.21	151.07 ± 14.02	14 ± 5
summer	500	58.13 ± 20.25	55.58 ± 3.76	141.67 ± 11.97	7 ± 2
summer	1500	33.75 ± 7.27	49.02 ± 11.27	96.33 ± 17.60	9 ± 2
winter	0	79.50 ± 35.14	57.34 ± 9.23	137.21 ± 21.32	3 ± 1
winter	500	50.62 ± 18.47	31.92 ± 0.34	81.85 ± 24.35	13 ± 4
winter	1500	46.67 ± 11.66	36.75 ± 7.47	113.50 ± 20.94	11 ± 5
spring	0	34.00 ± 4.74	62.92 ± 11.90	114.82 ± 14.99	8 ± 3
spring	500	74.57 ± 13.25	64.90 ± 6.44	115.63 ± 12.32	8 ± 5
spring	1500	41.00 ± 9.82	65.12 ± 14.85	91.80 ± 10.13	7 ± 2
control		-	-	-	11 ± 3

Table B3. Pre- and post treatment average % grass (*Calamagrostis canadensis*) cover (n=10) in relation to time of thinning aspen and season of cut. (± standard errors).

Time of thinning	Residual treatment density	Pre-treatment % grass cover	Post Treatment % grass cover
summer	0	9 ± 4	14 ± 5
summer	500	16 ± 6	7 ± 2
summer	1500	25 ± 9	9 ± 2
winter	0	19 ± 8	3 ± 1
winter	500	21 ± 6	13 ± 4
winter	1500	33 ± 10	11 ± 5
spring	0	30 ± 8	8 ± 3
spring	500	8 ± 3	8 ± 5
spring	1500	22 ± 8	7 ± 2
control		30 ± 9	11 ± 3